THE BOTANICAL GAZETTE

THE

BOTANICAL GAZETTE

EDITOR

JOHN MERLE COULTER

VOLUME LIII

JANUARY-JUNE, 1912

WITH TWENTY-SIX PLATES, EIGHTY-FIVE FIGURES, AND TWO PORTRAITS

THE UNIVERSITY OF CHICAGO PRESS
CHICAGO, ILLINOIS

Published
January, February, March, April, May, June, 1912

Composed and Printed By
The University of Chicago Press
Chicago, Illinois, U.S.A.

TABLE OF CONTENTS

DATES OF PUBLICATION

No. 1, January 17; No. 2, February 20; No. 3, March 15; No. 4, April 15; No. 5, May 15; No. 6, June 17.

ERRATA

P. 37, denominator of last formula, for $1+0.025$ read 1 ± 0.025.

P. 80, line [illegible] from top, for *tormanili* read *torminali*.

P. 80, line 30 from top, for *S. cornutum* read *Gymnosporangium cornutum*.

P. 80, line 32 from top, for Kochne read Koehne.

P. 81, line 7 from top, for *Trolli* read *Trollii*.

P. 126, omit BUREAU OF PLANT INDUSTRY, WASHINGTON, D.C.

P. 127, footnote 1, for LXV read LXVII.

P. 170, citation **22**, for 1909 read 1910.

P. 174, line 12 from top, for continued read contained.

P. 212, FIG. 2 is inverted.

P. 340, line 6 from bottom, for below read above.

P. 344, FIG. 2, for fig. 1*C* read fig. 1*B*.

P. 358, line 14 from top, for **46**: no. 9 read **46**: no. 5.

P. 391, citation **28**, for Howard read Houard.

P. 392, citation **31**, for Howard read Houard.

P. 418, last line, for *Iridoacoretum* read *Irido-acroetum*.

P. 435, citation **19**, for *pls*. read *pl*.

P. 435, citation **20**, for *pls*. read *pl*.

VOLUME LIII NUMBER 1

THE BOTANICAL GAZETTE

JANUARY 1912

MORPHOLOGY OF CERATOZAMIA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 153

CHARLES J. CHAMBERLAIN

(WITH PLATE I AND SEVEN FIGURES)

Southern Mexico, with its three genera of cycads (*Dioon*, *Ceratozamia*, and *Zamia*), is the principal cycad region of the western hemisphere. Two of these genera, *Dioon* and *Ceratozamia*, may be confined to Mexico. Occasional reports indicate a wider distribution, but both genera are so commonly cultivated in parks, both in Mexico and farther south, that descriptions, even when supported by specimens, would need the addition of observation in the field before habitats could be established. The first two descriptions of *Dioon spinulosum*, by DYER (1) and by EICHLER (2), were based upon cultivated specimens, and in the localities cited, Progreso and Cordoba, the species does not occur except in cultivation.

Ceratozamia has been reported beyond Mexico, but whether from observation in the field or from cultivated specimens, is uncertain. It grows wild at Chavarrillo, where it is associated with *Dioon edule*, but the plants are only seedlings with 2 or 3 leaves, except on Monte Oscuro, where there are some specimens large enough to bear cones. Between Jalapa and the extinct crater of Naolinco is a beautiful valley, and on the Jalapa side of the mountains which rise from this valley, large fruiting plants of *Ceratozamia* are abundant, but are limited to a rather narrow vertical

distribution, the altitude of which was not determined. Most of my material came from this region, largely from the hacienda of Señor Luis Caraza.

It is a pleasure to acknowledge my indebtedness to Governor Teodoro A. Dehesa and Mr. Alexander M. Gaw. During my first trip to Mexico in 1904, I failed to find any *Ceratozamia*, except a few seedlings at Chavarrillo, but after I had returned to Chicago, Governor Dehesa stationed an officer near cultivated plants in the park at Jalapa, and the officer questioned country people until he found one who knew where the plant grew wild. The region was the mountainous slope of the valley just referred to. After that, cones were easily secured, and for six years Mr. Gaw has sent cones at all seasons, until the series is very complete. Besides, I have been able to visit the valley myself, first in September 1906, and later in March 1908. On the latter trip, and again in September 1910, I found *Ceratozamia* in the mountains across the Papaloapan River at Tuxtepec, but the plants were rather small and bore no cones.

The plants in the valley, near Jalapa, I identified as *Ceratozamia mexicana*. There is considerable variation, aside from that which the leaves of cycads present at various stages in the growth of the plant, the variation appearing even in the cones, which show less variation than the vegetative structures.

In habitat *Ceratozamia* differs decidedly from *Dioon edule*, which grows in the open, exposed to blazing sunlight, while *Ceratozamia* is found in densely shaded places. The difference in light will be appreciated from the fact that a photographic plate which would be well exposed for *Dioon* in one-fifth of a second would require three minutes exposure for *Ceratozamia*. The *Ceratozamia* associated with *Dioon* at Chavarrillo always appeared stunted, with one, two, or three leaves, except on Monte Oscuro, where it is shaded by a dense growth of shrubs. Although *Ceratozamia* is not found in wet situations, it is associated with a luxuriant vegetation, while *Dioon edule* and the plants associated with it are xerophytic. The habitat of *Ceratozamia* resembles that of *Dioon spinulosum*, but the latter plant does not occur in the Jalapa region. In the Tuxtepex region *Ceratozamia* appears before the *Dioon* locality is reached, but I did not find the two growing together.

The trunk and leaves

The trunk of *Ceratozamia mexicana* seldom reaches 2 meters in length. It is rather slender, has an armor of persistent leaf bases,

FIG. 1.—*Ceratozamia mexicana* growing on a steep mountain side opposite Naolinco, near Jalapa.

and is often curved or prostrate. This habit is doubtless due to the fact that so many plants grow on steep slopes (fig. 1), for the apex

is always vertical. As in *Dioon*, the foliage display consists of two crowns, the latest fresh and bright green, while the previous one has a dull green color, or may appear pale or gray on account of the numerous small lichens which almost invariably incrust the leaves of the second crown. Few plants have more than 10 leaves in a crown, so that the foliage display of a large plant consists of about 20 leaves. On the larger plants the leaves are 1.5–2 meters in length and have 40–50 leaflets on each side, the leaflets measuring about 50 cm. in length and 2 cm. in width. The variation in the leaves of plants of different ages is readily seen from the fact that the first leaf of a seedling usually has 4 leaflets, sometimes only 2, and that these early leaves are shorter, thinner, and narrower than the leaves of old plants. Differences may also appear in the margins of the leaflets and in the spines on the lower part of the petiole, so that identifications based upon the leaf alone must be regarded with some suspicion.

A section of the adult stem shows that it is strictly monoxylic, with a very narrow zone of wood showing no growth rings (3).

The strobili

Strobili are not abundant, and occasionally Mr. GAW had difficulty in securing them. When very young, the ovulate and staminate strobili have the same general appearance, but even then they may be distinguished superficially by the much larger number of sporophylls on the staminate strobili, and by the fact that the staminate strobilus is somewhat conical, while the ovulate is cylindrical. At maturity the staminate strobilus is quite pointed, while the ovulate is very evenly cylindrical and is much larger.

THE STAMINATE STROBILUS

The staminate strobilus reaches its full size and sheds its pollen about the middle of March. The largest staminate strobili are about 20 cm. in length, but the average length is not more than 15 cm. A typical staminate strobilus is shown in fig. 2. The sporophylls are somewhat wedge-shaped, distinctly stalked, and are tipped by the two horny spines which give the name to the

genus. The sporangia are crowded over the entire abaxial surface of the sporophyll, with only a slight indication of any division into two groups by a sterile line through the center (fig. 3). The sori consist of three or four sporangia, with some two's and occasionally a single sporangium, the single sporangium being found more frequently at the top and bottom of the strobilus. The soral character is not always evident in a surface view, but is rather distinct after the pollen has been shed (fig. 3, *c*), and is easily seen by removing the sporangia or by examining sections (figs. 3, 4). Dehiscence begins in the peripheral sporangia of the sporophyll and progresses toward the axis of the cone, as shown in fig. 3, *b*. As in *Dioon edule*, the wall of the sporangium is thin at the sides and thicker at the top, with a thick-walled outer layer of cells and thin-walled cells between this and the sporogenous tissue. The dehiscence is marked by two rows of thin-walled cells which contrast sharply with the thick-walled cells of the rest of the outer layer. The cells of the outer layer are elongated parallel to the dehiscence, so that in a section at a right angle to the dehiscence they are almost square in outline (fig. 5), while in a sec-

FIG. 2.—Staminate strobilus; $\times \frac{1}{2}$.

tion parallel to the dehiscence the length is several times as great as the breadth.

THE OVULATE STROBILUS

The ovulate strobilus is cylindrical in outline, and when mature is green and smooth. There is such variation in the size and general appearance of the strobilus that if one considered only the extremes he could easily describe new species. What may be regarded as extremes in the appearance of large cones is represented in figs. 6 and 7. The largest cone noted in several year's collections was 33.5 cm. in length and 11 cm. in diameter, and the smallest measured 21×8.5 cm. The average size is about 26.3×9.7 cm.

a

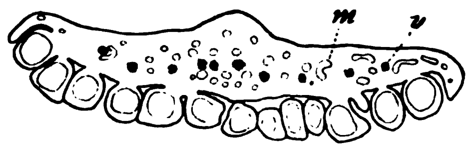
FIG. 3.—Staminate sporophylls: *a*, before dehiscence; *b*, dehiscence has taken place in the upper half but not yet in the lower; in *c*, nearly all the sporangia have shed their pollen; ×2.

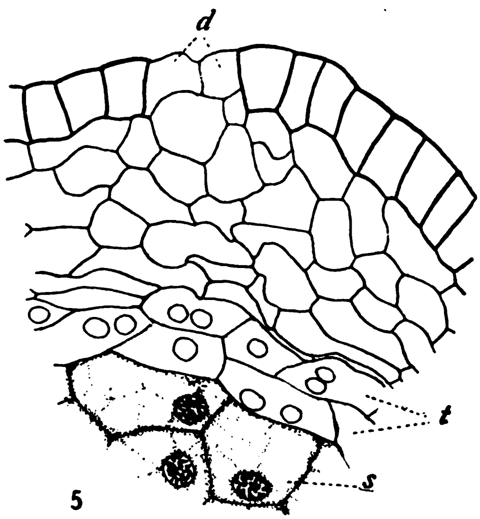
The sporophylls appear to be arranged in vertical rows, and the number of sporophylls can be determined with considerable accuracy by counting the number of rows and number of sporophylls in a row, but the arrangement is strictly spiral. The lowest number of sporophylls observed was 72, in 8 rows with 9 in a row; and the highest number was 182, in 14 rows with 13 in a row; an average computed from 12 well developed cones was 11 rows with 11 in a row. The number of sporophylls, therefore, varies from 72 to 182, with 121 as an average; and the number of ovules varies from 144 to 364, with an average of 252, since each sporophyll bears two ovules.

The two hard spines or horns, which are similar to those on the microsporophyll, are always conspicuous, and they are so stiff and sharp that they make a large cone an uncomfortable object

to hold in the hand. At the top of the cone the sporophylls often bear 3 spines and sometimes as many as 5 or 6, the arrangement and vascular connections making it evident that they are reduced pinnae. These sporophylls and some reduced sporophylls at the base of the strobilus bear no ovules.

The young ovules are softly pubescent, but become perfectly smooth at maturity. They are small, seldom reaching more than 2.6 cm. in length and 1.8 cm. in breadth. When very young, and also at maturity, they are white, but during intermediate stages there is a delicate pink color, not very conspicuous from the outside, because the color is in the layer which is to become stony, and consequently is masked by the outer fleshy layer. The stony layer is much thinner than in *Dioon*, and can be cut with a pocket knife, even when the seed is ripe. There is no pit in the base of the stony layer, as in *Dioon edule*, but rather a slight projection, so that the two species can be distinguished from each other by the character of the base of the stony layer.





FIGS. 4 AND 5.—Fig. 4, Transverse section of staminate sporophyll with its sporangia; *m*, mucilage ducts; *v*, vascular bundles; ×10; fig. 5, Portion of wall of microsporangium: *d*, dehiscence; *t*, tapetum; *s*, sporogenous tissue; ×375.

The general distribution of the vascular system of the ovule is as in *Dioon;* in the outer fleshy layer there is a system of unbranched bundles extending from the base of the ovule almost to the micropyle, and in the inner fleshy layer a system of bundles which branch

FIGS. 6 AND 7.—Fig. 6, ovulate strobilus with large sporophylls; $\times \frac{1}{2}$, fig. 7, ovulate strobilus with smaller and more numerous sporophylls; $\times \frac{1}{2}$.

dichotomously and occasionally anastomose. The number of bundles in the outer system varies from 8 to 10, with 9 as the most usual number. About 6 bundles pass through the stony layer to the inner fleshy layer, where they branch repeatedly. In the stalk of the sporophyll there is a single bundle passing toward each ovule; this bundle branches once in the spreading part of the sporophyll, and each branch contributes to both the inner and the outer vascular systems of the ovule.

Both strobili and ovules may reach the maximum size in greenhouse specimens where there has been no possibility of pollination. This seems to be the rule in *Ceratozamia*, although I have seen two or three greenhouse strobili in which nearly all the ovules were abortive.

The male gametophyte

Records in regard to the time of shedding pollen are not very complete. In two staminate cones sent from the Almolongo Valley, near Jalapa, December 5, 1906, arriving in Chicago December 12, the pollen tetrads had already shaken apart, but the exine had not begun to look yellow. In two cones sent from the same place February 5, 1907, and reaching Chicago 7 days later, the pollen was yellow, but the sporangia had not yet dehisced. Four cones from Chiltoyac, near Jalapa, reached Chicago March 10, 1906, and the largest of the four began to shed its pollen 2 days later. A cone of *Ceratozamia mexicana* var. *longifolia*, sent on April 14, 1909, from the Missouri Botanical Garden by Professor TRELEASE, reached Chicago the following day. Much of the pollen was already shed.

While there is considerable variation in the time at which the pollen is shed, the condition of the pollen at the time of shedding is always the same; there is a tube cell, a well developed, persistent prothallial cell, and a generative cell which will later give rise to the stalk and body cells.

The mature pollen grain of *Ceratozamia mexicana* can be distinguished from that of *Dioon edule* by the spore coats, the exine and intine being quite uniform throughout in *Ceratozamia*, while in *Dioon* the exine is much thicker at the base of the spore and the intine much thickened along the sides.

The pollen grain, as it is shed, is shaped like a kernel of coffee,

with a deep furrow across the top, due to the fact that the exine does not cover the entire surface, but is lacking at the apex of the spore, so that when the spore contracts in the drying out which precedes shedding, the elastic exine springs together until the opposite sides touch, thus making it look as if the exine covered the entire spore. When placed in water or in a nutrient solution, the spore immediately begins to swell, and in a few minutes becomes quite spherical. In a 10 per cent solution of cane sugar, or in the juice of either fresh or preserved pears, germination takes place at once. Within 24 hours the intine begins to protrude, and in 3 or 4 days some of the tubes are two or three times as long as the pollen grain. In cultures there is a considerable elongation of the pollen tube and some increase in the amount of starch, but I have never succeeded in finding a division of the generative cell. The beginning of germination, as it appears in a 10 per cent sugar solution, is shown in figs. 8, 9, and 10.

The pollen tube is quite characteristic, and easily distinguishes *Ceratozamia* from any cycads yet described. As in other cycads, the brown roof of the pollen chamber, with the nucellar beak in its center, is present, but the brown lines due to the haustoria of pollen tubes are scarcely visible, and even in abundantly pollinated strobili the brown spot itself is seldom more than 1 mm. in diameter. That there are haustoria, 2–3 mm. long and lying just beneath the surface of the nucellus, is evident from a glance at a section, but they do not cause conspicuous brown lines upon the surface.

The most striking feature of the pollen tube is a series of secondary haustoria developed from various parts of the enlarged basal end of the pollen tube (fig. 11). As soon as the pollen grain is shed, the primary haustorium, as the familiar haustorium of cycads might be called, begins to develop, and with little or no branching reaches a length of 1–2 mm., its course lying just beneath the surface of the nucellus. The secondary haustoria are developed much

ie same diameter as the primary haus-
in outline and usually branch. Their
the archegonia, and their development
.he division which is to form the ventral

canal nucleus and egg nucleus, while the archegonial chamber is still quite shallow and the pollen chamber only half way through the nucellus, their tips have already reached the megaspore membrane. They contain starch and occasionally the tube nucleus wanders into one of them, but the tube nucleus, at the stage shown in figs. 11 and 12, is almost invariably found in the enlarged portion of the tube and is usually near the body cell. Only in very early stages is it found in the primary haustorium.

As the tissue of the nucellus breaks down beneath the advancing pollen tubes, the secondary haustoria, especially those extending directly downward, become bent and twisted and finally appear as an irregular tangle pressing against the megaspore membrane (fig. 12). The tissues of the nucellus disorganize so rapidly that the secondary haustoria do not hold back the basal end of the tube, but advance with it. The disorganization which forms the pollen chamber is very extensive, including not only the region occupied by the basal ends of the tubes, but finally all the tissues in the region of the secondary haustoria.

The division of the generative cell into the stalk and body cells, a division which I was not able to secure in cultures, takes place quite promptly after the pollen grains have reached the pollen chamber, probably within a week after pollination. From a record of various cones of various seasons, the time at which the body cell divides shows considerable variation, the division being noted as early as the middle of June, and as late as the first of August. The most usual time is the first week in July.

In nearly all cases, two sperms are produced from each body cell, but four sperms were found in a few cases. In two cases, four sperms were found in isolated pollen tubes mounted without sectioning; in one case, four were found in one tube in serial sections; and in another case, shown in fig. 13, the body cell had divided, forming two cells, each with the aspect of a body cell and with two blepharoplasts, so that there is no doubt as to the manner in which the four sperms are formed.

At the division of the body cell, the mitotic figure is small and entirely intranuclear during the metaphase, but after the nuclear

membrane has broken down in the anaphase, the spindle develops enormously and occupies a broad zone between the two daughter nuclei (fig. 14).

The two cells formed at this division are sperm mother cells, as we have already shown in case of *Dioon edule* (4). In each of the sperm mother cells a sperm is formed, and subsequently escapes by the breaking down of the wall of the mother cell (fig. 15).

The blepharoplast is the largest yet recorded for any cycad, seldom measuring less than 20 μ in diameter, and occasionally reaching a diameter of 27 μ, while blepharoplasts 25 μ in diameter are not rare. The enormous size of this blepharoplast will be appreciated when one remembers that nuclei in the meristematic region of the familiar onion root tip (*Allium Cepa*) seldom measure more than 15 μ in diameter and rarely reach a diameter of 20 μ. Naturally, this blepharoplast is favorable for study, and from the collections of six years the series of stages is very complete, but since such a study should be strictly cytological, I shall reserve for a special paper the division of the body cell and the behavior of the blepharoplast in the formation of the ciliated spiral band. During the formation of the spiral band, remarkable changes take place in the nucleus of the sperm, and these will also be considered in the special paper. For the present, we need only say that the solid blepharoplast becomes vacuolated, and breaks up into a mass of granules from which the greater part of the ciliated band is formed. The band starts in contact with the nucleus, the lowest turn being formed first, and ends at the apex of the sperm. The most usual number of turns of the spiral band is 7, but 6 and also 7.5 are found occasionally. The spiral may be either right or left, or better, it may be formed either in the direction of the hands of a clock or contra clockwise. The actual direction is usually with the hands of the clock, but camera lucida drawings will show the contra clockwise spiral, since the microscopic image is always reversed. In many instances it was possible to determine the direction of the spiral in both of the two sperms from the same body cell, and in most cases one showed the clockwise and the other the contra clockwise direction.

The sperms of *Ceratozamia* are not so large as those of *Zamia* or

Dioon, the average measurements of sperms in the pollen tube being 220 μ in diameter and 185 μ in length from apex to base. The sperms of *Zamia floridana*, as described by WEBBER (5), reach a diameter of 306 μ and a length of 332 μ, and those of *Dioon edule* measure 230 μ in diameter and 300 μ in length. The sperms of *Cycas* and *Microcycas* are smaller.

The sperms were often examined in the living condition. They are easily visible to the naked eye, and with a pocket lens one can see the more general features of their movements, but an examination under low powers of the microscope is more satisfactory. When exposed to the air, the pollen tubes soon burst, the sperms seldom swimming longer than 15 minutes after the ovules are opened, but when the ovules are cut transversely, the female gametophyte removed, and the cut end placed in a drop of sugar solution on a slide, the tubes may be examined for a few seconds at a time and thus allow a more prolonged observation. Just how long the sperms are in the motile condition was not determined, for sperms which have not begun to move when an ovule is opened may suffer from the shock, and when sperms are already moving it cannot be determined how long they have been motile. Movements of individual sperms have been observed for 6 hours.

The movements are like those described for *Dioon edule*, a forward movement accompanied by a rotation upon the axis. The sperms swim rapidly, bumping against each other and against the sides of the tube. When swimming straight ahead the apex is stretched out in front (fig. 16), but when the sperm strikes anything the apex is often drawn in suddenly, with a movement reminding one of the sudden retreat of a *Vorticella*. So far as the form is concerned, the drawings of three sperms shown in figs. 15 and 16 might have been made from a single sperm at intervals of a few seconds. There is also a slower, amoeboid movement of both cytoplasm and nucleus. The contour of the nucleus is very irregular and is constantly changing. Slender prolongations of the nucleus may reach nearly or quite to the ciliated band.

A few attempts were made to determine whether the sperms are chemotactic or not, but no results were obtained. MIYAKE (8) reported that the sperms of *Cycas* show no chemotropism, and

while his results were negative, I am inclined to believe they are entirely correct, for the entrance of the sperm into the egg in both *Ceratozamia* and *Dioon* seems to be independent of any chemotactic phenomena.

The female gametophyte

If strobili were numerous, *Ceratozamia* would be favorable for a study of the origin and development of the megaspore, for the strobili break through the bud scales at a very early stage. The earliest stage in any material shows free nuclear division in the megaspore. The general course of development is about the same as in *Dioon edule* (9), the principal differences being that structures are smaller, the mature gametophyte being about 2.5 cm. in length, and the archegonia at the time of fertilization seldom reaching a length of more than 3 mm.

WARMING (10) in 1877 reported a ventral canal cell in *Ceratozamia robusta*, but soon concluded that he had been mistaken. It is not surprising that he was in doubt, for the ventral canal nucleus in *Ceratozamia mexicana* is very small and usually disorganizes very promptly. The relative sizes of the ventral canal nucleus and the egg nucleus are shown in fig. 17, while 17*a* is a detailed drawing of the ventral canal nucleus shown in fig. 17. It is of special interest to note that the ventral canal nucleus does not always disorganize, but may enlarge, as it sometimes does in *Pinus* (11) and *Ginkgo* (12), and in such cases it is very probable that the egg may be fertilized by the ventral canal nucleus. I have seen two cases in *Ceratozamia* in which a large nucleus, looking like the nucleus of the sperm, was only a short distance from the egg nucleus, but no ciliated band could be found in the egg and the neck cells were still turgid. The objection is easily made that the failure to find the ciliated band is only negative evidence, but the band is so large and so persistent, that to one familiar with cycads the failure to find it at this early stage is conclusive proof that no band is present. Of course it might be suggested that only the nucleus had entered the egg, the band remaining outside, but in many cases the sperm, with the ciliated band, was observed inside the egg, sometimes being plainly visible in late free nuclear stages of the proembryo (fig. 20).

A strong reason for believing that fertilization is sometimes effected by a ventral canal nucleus is found in a paper by VAN TIEGHEM (13) published in 1870. He secured four seedlings, the result of fertilization of the ovules of *Ceratozamia longifolia* by "the pollen of *C. mexicana*, which had been preserved for three years." VAN TIEGHEM speaks of these seedlings as hybrids, but I do not believe the pollen of *Ceratozamia* will live for three years. Pollen of *C. mexicana*, shed April 22, 1909, in cultures started on that date and also a week later, germinated immediately, but in cultures made a month later from the same collection of pollen, the grains simply became spherical, but would not germinate. In January 1911, I pollinated two cones of *Zamia Ottonis* with some of the same pollen, at about the same time pollinating another cone of *Z. Ottonis* with pollen of *Z. floridana*. I have not yet examined the cones, except to note that they are in fine condition, preferring to wait for the later embryo and seedling stages, if there should be any. At the time of this pollination I again made cultures of the old pollen of *Ceratozamia*, but not a single pollen grain germinated, and recently I repeated the attempt, but no germination occurred. The old pollen is doubtless dead, and VAN TIEGHEM's seedlings were parthenogenetic or were the result of fertilization by a ventral canal nucleus. I might mention here that I have preparations of *Encephalartos* from a greenhouse specimen where there had been no possibility of pollination, in which the ventral canal nucleus has become greatly enlarged and has moved toward the egg nucleus. I should not be surprised to find occasional seedlings from cycads in greenhouses where there has been no pollination.

The archegonial chamber is conspicuous before the pollen tubes are half way through the nucleus, and during the early stages in its development it contains a fluid, doubtless secreted by the gametophyte, for the megaspore membrane is torn loose from the bottom of the chamber. At the time of fertilization the chamber, although moist, does not contain liquid.

The megaspore membrane is thin, only 2.5–3 μ in thickness. It has about the same structure as in *Dioon edule* (9), a comparatively homogenous inner layer beset with an outer layer of irregular club-shaped bodies. These bodies, which in some gymnosperms

are prismatic on account of pressure, are so scattered that they are nearly always round in vertical view (fig. 18).

FERTILIZATION

All observations indicate that fertilization takes place as in *Dioon edule*, the liquid from the pollen tube lowering the turgidity of the neck cells of the archegonium, so that they allow the escape of a portion of the cytoplasm of the upper part of the egg, thus producing a vacuole which draws the sperm into the egg.

In numerous instances the sperms were observed within the egg, occasionally two or three sperms entering the same egg, but in such cases the extra sperms remain at the top of the egg, and the nuclei do not slip out from the cytoplasmic sheath. The actual fusion of the sperm and egg nuclei was not observed, and consequently it cannot be stated at present whether they fuse in the resting condition or behave as in *Pinus*.

Embryo

The extent of the free nuclear period in the development of the embryo was not determined, the latest stage observed being the 256-nucleate stage shown in fig. 19. No stages were found between this and the young embryos with suspensors shown in figs. 20–22.

The membrane of the egg, often with traces of the archegonium jacket clinging to it, persists for a long time. Five such membranes, each with a suspensor coming from its base, are shown in fig. 20. In this case four of the suspensors, each with an embryo at its tip, have united, forming a single suspensor with a single embryo. The other suspensor, with its embryo, advanced only half as far before it ceased to develop. In another case (fig. 21), two suspensors with their embryos have united, and the third, although smaller, has reached about the same length. In another case (fig. 22), all the suspensors and embryos developed separately. These cases are characteristic. A single embryo may be the product of one fertilization or may come from several eggs. In early stages, the young embryos are more or less irregular (fig. 23), but regularity is soon established.

The strobili disorganize and shed their seeds very early, often

before the stage shown in figs. 20–23 is reached, and consequently before the cotyledons have begun to be differentiated. Sister Helen Angela (14), noting this fact and finding traces of vascular tissue which might belong to the missing cotyledon, rotated seeds on a klinostat from the time the seeds were liberated until the embryos were mature. Such seeds showed two cotyledons as in other cycads, so that the single cotyledon of *Ceratozamia*, as it is found in nature, is due to a suppression of one of the cotyledons, doubtless on account of the early liberation of the seeds.

The seeds of *Ceratozamia* germinate as soon as they are ripe, a feature which I have noted in *Dioon edule*, *D. spinulosum*, *Zamia floridana*, *Cycas circinalis*, *Macrozamia Fraseri*, and *Stangeria paradoxa*. Very probably the seeds of all cycads may germinate without any resting period; but seeds of *Ceratozamia*, which had become dry in the laboratory, were planted a year later and germinated readily. Seeds of *Dioon edule* which had been in the laboratory for nearly three years germinated. The most favorable time for germination is that immediately following maturity, for at this time nearly all seeds of both *Ceratozamia* and *Dioon* will germinate, but after a lapse of a few months the proportion of seeds which will germinate steadily diminishes.

Summary

1. *Ceratozamia mexicana* grows best in well shaded mesophytic conditions.

2. Any individual in passing from the seedling to the adult stage shows such a progressive change in its leaves, the leaflets becoming larger, broader, thicker, and more numerous, that descriptions of species based largely upon leaves are open to suspicion.

3. The ovulate strobilus shows considerable variation in the size and number of its sporophylls.

4. In addition to the primary haustorium, a system of secondary haustoria is developed later from the basal portions of the pollen tube. There are regularly two sperms, but occasionally four are produced.

5. A small ventral canal nucleus is present, but occasionally it enlarges and may fertilize the egg. It is suggested that this

may explain the so-called hybrids obtained by VAN TIEGHEM. In most cases fertilization occurs in the usual way.

6. Both suspensors and young embryos may unite, so that from five fertilized eggs there may come one to five embryos. In the mature seed, as found in nature, there is one embryo with a single cotyledon.

THE UNIVERSITY OF CHICAGO

LITERATURE CITED

1. DYER, W. T., THISTLETON, Cycadaceae, in Biologia Centrali-Americana. Botany **3**:190–195. 1882–1886.
2. EICHLER, A. W., Ein neues *Dioon*. Gartenflora **2**:411–413. 1883.
3. CHAMBERLAIN, C. J., The adult cycad trunk. BOT. GAZ. **52**:81–104. *figs. 20.* 1911.
4. ——, Spermatogenesis in *Dioon edule*. BOT. GAZ. **27**:215–236. *pls. 15–18.* 1909.
5. WEBBER, H. J., Spermatogenesis and fecundation of *Zamia*. U.S. Dept. of Agric., Bur. Pl. Ind., Bull. No. 2. pp. 100. *pls. 7.* 1901.
6. IKENO, S., Untersuchungen über die Entwickelung der Geschlechtsorgane und die Vorgang der Befruchtung bei *Cycas revoluta*. Jahrb. Wiss. Bot. **32**:557–602. *pls. 8–10.* 1898.
7. CALDWELL, O. W., *Microcycas calocoma*. BOT. GAZ. **44**:118–141. *pls. 10–13.* 1907.
8. MIYAKE, K., Ueber die Spermatozoiden von *Cycas revoluta*. Ber. Deutsch. Bot. Gesells. **24**:78–83. *pls. 6.* 1906.
9. CHAMBERLAIN, C. J., The ovule and female gametophyte of *Dioon*. BOT. GAZ. **42**:321–358. *pls. 13–15.* 1906.
10. WARMING, E., Recherches et remarques sur les cycadées. Oversigter Vidensk. Selsk. Forh. 1877.
11. CHAMBERLAIN, C. J., Oogenesis in *Pinus Laricio*. BOT. GAZ. **27**:268–280. *pls. 4–6.* 1899.
12. IKENO, S., Contribution à l'édule de la fécundation chez le *Ginkgo biloba*. Ann. Sci. Nat. Bot. **13**[8]:305–318. *pls. 2, 3.* 1901.
13. VAN TIEGHEM, PH., Recherches sur le symétrie de structure des plantes vasculaire. Ann. Sci. Nat. Bot. **13**[5]:1–314. *pls. 3–8.* 1870.
14. ANGELA, SISTER HELEN, The embryo of *Ceratozamia;* a physiological study. BOT. GAZ. **45**:412–416. *figs. 7.* 1908.

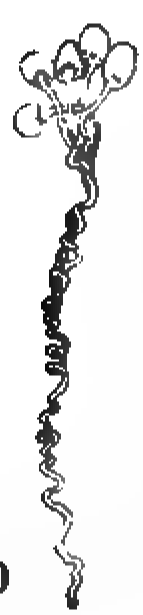
8

9

17

17 *a*

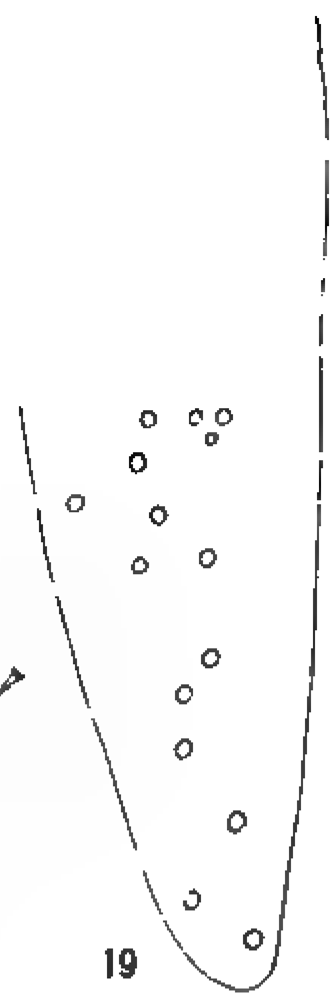
1



20

21

22



19

CHAMBERLAIN on CERATOZAMIA

EXPLANATION OF PLATE I

(Figs. 1–7 are text cuts)

Ceratozamia mexicana

FIG. 8.—Pollen grain beginning to germinate in a sugar solution; beneath the tube nucleus is the generative cell which is to produce the stalk and body cells; beneath this and resting upon the intine is the single persistent prothallial cell; the spherical bodies are starch grains; ×730.

FIG. 9.—Like the preceding figure, but there has been some plasmolysis, and at the right side of the figure, toward the top, the intine has pulled loose from the exine; ×730.

FIG. 10.—Germinating pollen grain drawn from living material; ×730.

FIG. 11.—Nucellus and part of female gametophyte with archegonia; the pollen tube at the right shows the primary haustorium just beneath the upper surface of the nucellus, and farther down, opposite the body cell, a branching secondary haustorium; the lightly dotted area above the archegonia represents the liquid filling the archegonial chamber and pressing up the megaspore membrane, represented by the dark line; ×14.

FIG. 12.—Nucellus at a later stage showing behavior of secondary haustoria; ×14.

FIG. 13.—Pollen tube which would have produced four sperms; a single unbranched secondary haustorium extends obliquely downward; ×130.

FIG. 14.—Two young sperm mother cells showing the remnants of the broad spindle and the ciliated band just beginning to form; ×180.

FIG. 15.—Two sperms about to escape from their mother cells; ×130.

FIG. 16.—Mature sperm; ×180.

FIG. 17.—Part of archegonial chamber and upper part of the archegonium, showing the small ventral canal nucleus and the egg nucleus; ×25.

FIG. 17*a*.—Detailed drawing of the ventral canal nucleus shown in the preceding figure; ×475.

FIG. 18.—Megaspore membrane with parts of two adjacent endosperm cells; ×833.

FIG. 19.—Free nuclear stage of proembryo; the sheath and ciliated band of the sperm are shown at the top; ×27.

FIG. 20.—One embryo formed by the fusion of four; the fifth embryo stopped developing part way down the suspensor region; ×1.5.

FIG. 21.—Three suspensors with two embryos; ×1.5.

FIG. 22.—Each suspensor has an embryo at its tip; ×1.5.

FIG. 23.—Young embryo showing irregular outline of an embryo formed by fusion of two or more embryos; ×1.5.

THE WILTING COEFFICIENT AND ITS INDIRECT DETERMINATION[1]

LYMAN J. BRIGGS AND H. L. SHANTZ

THE WILTING COEFFICIENT

If the roots of a plant are well established in a mass of soil, the plant gradually reduces the water content until permanent wilting occurs. The water remaining in the soil under this condition has been termed non-available by previous writers. We have found, however, that plants can reduce the soil moisture content somewhat below the point corresponding to the permanent wilting of the leaves, so that the water content at the wilting point is not strictly non-available. In fact, this loss of water from the soil to the air goes on through the plant tissues even after the death of the plant, and appears to be limited only by the establishment of a state of equilibrium between the soil and the air. The plant during the drying stage acts simply as a medium for the transference of water, and while the rate of loss is reduced, the final result is the same as if the air and soil were in direct contact. By means of the wax seal method, which effectually prevents all direct loss of water from the soil, we have been able to demonstrate conclusively that there is a continued loss of water from the soil through the plant long after wilting occurs. This is shown by the results given in the accompanying table (table I).

The wheat seedlings were grown in sealed glass pots containing about 200 grams of soil. The second column of the table gives the water content of the soil corresponding to the wilting of the plants. The third column gives the number of days intervening between the wilting and the death of the plants, at which time the moisture content of the soil had been materially reduced, as shown in the fourth column. A still greater loss of water occurred during the subsequent period, at the end of which the moisture content of the

[1] Published by permission of the Secretary of Agriculture.

soil had been reduced to the point indicated in the last column of the table. The mean moisture content of the soil at the death point had been reduced to 85 per cent of the water content at the wilting point, while the mean soil moisture content at the end of the experiment was only 63 per cent of that at the wilting point.

TABLE I

THE WATER CONTENT OF THE SOIL IN SEALED POTS AT THE WILTING POINT AND DEATH POINT FOR KUBANKA WHEAT, AND AT A LATER PERIOD

Pot no.	Wilting point	Time interval in days	Death point	Time interval in days	Final percentage
4..........	7.0	28	5.2	126	3.1
6..........	7.9	25	5.9	126	2.6
7..........	7.0	25	5.5	126	3.5
8..........	6.6	19	6.4	126	4.9
9..........	7.1	27	5.9	134	4.8
10..........	7.8	27	6.9	134	5.9
11..........	6.9	19	5.9	126	4.3
12..........	7.3	27	6.6	134	5.9
13..........	8.0	27	6.9	37	6.1
14..........	7.3	27	6.2	134	4.9
Mean ...	7.3		6.2		4.6

The water remaining in the soil at the time the plant wilts cannot then with propriety be termed "non-available." We have shown that a considerable part of it is available, being absorbed by the roots of the dying or dead plant and evaporated from its aerial tissues, this process becoming slower and slower as the water content is reduced, and reaching its final limit in a condition of equilibrium between the soil and the air.

It appears advisable, therefore, to use a more specific term for the moisture content of the soil corresponding to the wilting point of a plant, and we have employed the term "wilting coefficient" in this sense in the present paper. The wilting coefficient is defined then as the percentage water content of a soil when the plants growing in that soil are first reduced to a wilted condition from which they cannot recover in an approximately saturated atmosphere without the addition of water to the soil.

The method used in determining the wilting coefficient has been

described in a previous paper.[2] The plants are grown in small glass pots, evaporation from the soil surface being prevented by means of a wax seal. The conditions are maintained as nearly uniform as possible until the plants wilt permanently. Special care is taken to secure uniformity in the texture and water content of the soil mass before filling the pots. Sudden fluctuations in soil temperature are avoided by keeping the pots in a water bath during the growth of the plants. When these precautions are observed, the physiological measurement of the wilting coefficient is as accurate as the physical methods of measuring the moisture retentiveness of a soil. It is shown in the paper already referred to that the probable error of the mean wilting coefficient for 13 or more determinations is only about 0.005 of the actual determinations in the case of loam and clay soils. For single determinations the probable error is about 0.02 of the mean value. In the case of sands, the corresponding probable error is about twice as great as in the loam and clay soils.

INDIRECT DETERMINATION OF THE WILTING COEFFICIENT

In all plant investigations in which the water supply may become a limiting factor, it is necessary to determine from time to time the amount of moisture in the soil available for plant growth. If we make the specific assumption that growth cannot take place unless the water content of the soil is equal to or exceeds the wilting coefficient, then the percentage of soil moisture available for growth at any time is represented by the actual moisture content minus the wilting coefficient. If the actual water content is less than the wilting coefficient, then the percentage of available water is negative, that is, water to this amount must be added to the soil before any growth can take place.

The percentage of moisture in the soil at the wilting point varies greatly in different types of soil. This appears to have been established first by SACHS,[3] and has been further investigated

[2] BRIGGS, L. J., and SHANTZ, H. L., A wax seal method for determining the lower limit of available soil moisture. BOT. GAZ. 51:210–219. 1911; also The wilting coefficient for different plants and its indirect determination. U.S. Dept. Agric., Bur. Pl. Ind., Bull. 230. 1911.

[3] SACHS, J., Bericht über die physiologische Thätigkeit an der Versuchstation in Tharandt. Landw. Versuchs-Stat. 1:235. 1859.

by GAIN,[4] HEINRICH,[5] and more recently by HEDGCOCK.[6] No quantitative correlation between the soil texture and the non-available moisture was established, and only in the case of a few soil types was the non-available moisture recorded.

In field studies of soil moisture, determinations of the total water content can easily be made. The errors which enter into the determination of the wilting coefficient under field conditions are very great, due to the direct evaporation from the soil, local variation in soil texture, and non-uniform root distribution, combined with the difficulty of determining the exact wilting point when the roots occupy a large soil mass. Furthermore, it is only during periods of extreme drought that conditions are favorable for wilting coefficient determinations in the field. In view of these difficulties, it becomes important to ascertain whether the wilting coefficient can be determined by an indirect method based upon the relationship of the wilting coefficient to the moisture retentiveness of the soil as measured by physical methods.

Accordingly we have compared the wilting coefficient with the moisture equivalent, the hygroscopic coefficient, the moisture holding capacity, and mechanical analysis for a series of soils ranging from sands to clays. In the wilting coefficient determinations Kubanka wheat (Grain Investigations no. 1440) has been used as an indicator. The results of these comparisons are given in the following sections:

RELATION OF THE WILTING COEFFICIENT TO THE MOISTURE EQUIVALENT

The moisture equivalent of the soil is the percentage of water which it can retain in opposition to a centrifugal force 1000 times that of gravity.[7] In making the determinations the soils are

[4] GAIN, E., Action de l'eau du sol sur la végétation. Rev. Gén. Botanique 7:73. 1895.

[5] HEINRICH, R., Zweiter Bericht über die Verhältnisse und Wirksamkeit des Landwirtschaftlichen Versuchs-Station zu Rostock, 1894, p. 29.

[6] HEDGCOCK, G. G., The relation of the water content of the soil to certain plants, principally mesophytes. Bot. Survey Nebraska. VI. Studies in the vegetation of the State II. 1902:5–79.

[7] BRIGGS, L. J. and MCLANE, J. W., The moisture equivalent of soils. U.S. Dept. Agric., Bur. Soils, Bull. 45. 1907; also, Moisture equivalent determinations and their application. Proc. Amer. Soc. Agronomy (1910) 2:138–147. 1911.

placed in perforated cups and moistened with an amount of water in excess of the amount they can hold in opposition to the centrifugal force. After standing 24 hours, the cups are placed in a centrifugal machine, which is operated at a constant speed so chosen as to exert a force 1000 times that of gravity upon the soil moisture. Each soil then rapidly loses water until the capillary forces are increased sufficiently to establish equilibrium with the centrifugal force employed. The moisture content of each soil is now not only in equilibrium with a force 1000 times that of gravity, but is also in capillary equilibrium with every other soil which has been similarly treated, so that if the soils are placed in capillary contact in any combination whatever, no movement of water from one soil to another will occur. The moisture content of each soil under these conditions is the moisture equivalent of that soil. This method, then, provides a means of determining and comparing the retentiveness of different soils for moisture when acted upon by a definite force, which is measured in absolute terms and is reproducible within narrow limits.

In the accompanying table (table II) is given a comparison of the wilting coefficient and the moisture equivalent for a series of soils ranging in texture from a coarse sand to a clay. The names applied to the soils have been determined from the mechanical analyses in accordance with the soil classification table used by the Bureau of Soils.[8] The soils are arranged in the order of increasing moisture equivalents. For the moisture equivalent determinations we are indebted to Mr. J. W. McLane. All moisture determinations are expressed as percentages of the dry weight of the soil used.

The moisture equivalent determinations given in the table represent in each case the mean of two determinations. The number of wilting coefficient determinations made upon each soil is shown in the fourth column, and the mean of these determinations is given in the fifth column. The last column gives the ratio of the moisture equivalent to the wilting coefficient for each soil.

It will be seen from an inspection of the table that the soils used in the comparison show a wide range in moisture retentiveness,

[8] Soil Survey Field Book, 1906.

the moisture equivalent increasing from 1.6 per cent in sand to over 30 per cent in the clay loam; while the wilting coefficient ranges from 0.9 per cent in sand to 16.5 per cent in the clay loam. The mean ratio of the moisture equivalent to the wilting coefficient for all the soils examined is 1.84. The probable error of this mean is ±0.013; that is to say, considering the series to be representative of soils as a whole, the chances are even that if a similar series of determinations were made the mean of the ratios would fall between 1.827 and 1.853.

TABLE II

THE RELATION OF THE WILTING COEFFICIENT TO THE MOISTURE EQUIVALENT IN SOILS RANGING FROM SAND TO CLAY

No.	Soil type	Moisture equivalent	Wilting coefficient		Ratio of moisture equivalent to wilting coefficient
			No. dets.	Average	
7............	Coarse sand	1.6	11	0.9	1.78
2............	Fine sand	4.7	16	2.6	1.81
8............	Fine sand	5.5	3	3.3	1.67
9............	Fine sand	6.7	2	3.6	1.86
3............	Sandy loam	9.7	9	4.8	2.02
10............	Sandy loam	11.9	3	6.3	1.89
4............	Fine sandy loam	18.1	13	9.7	1.87
12............	Loam	18.9	3	10.3	1.83
A............	Sandy loam	19.6	1	9.9	1.98
B............	Fine sandy loam	19.9	1	10.8	1.84
C............	Fine sandy loam	22.1	1	11.6	1.90
5............	Loam	25.0	12	13.9	1.80
D............	Loam	27.0	1	15.2	1.78
13............	Clay loam	27.4	2	14.6	1.88
14............	Clay loam	29.3	4	16.2	1.81
E............	Clay loam	30.0	1	16.5	1.82
6............	Clay loam	30.2	16	16.3	1.85

Mean...1.84

Probable error of mean.........±0.013

It will be noted that the greatest departures in the ratios are found among the sandier soils. This is due to the fact that a slight experimental error in determining either the moisture equivalent or the wilting coefficient affects the ratio markedly owing to the small percentages of moisture with which we are dealing in these soils.

The significant feature of the results here presented is the fact that through the wide range of moisture retentiveness exhibited

by the soils employed, the ratio of the moisture equivalent to the wilting coefficient appears to be constant within the limits of experimental error. In other words, two determinations of the moisture retentiveness of these soils, one physical and the other physiological, show a linear relationship which is independent of the texture of the soil. The relationship is expressed by the following formula:

$$\frac{\text{Moisture equivalent}}{1.84 \pm 0.013} = \text{wilting coefficient.}$$

In order to compare the available moisture content of one soil with that of another, we must know or be able to estimate accurately the wilting coefficient of each soil. The minimum limit of moisture available for growth is the datum line from which all comparisons should be made. This datum can be established directly by wilting coefficient measurements, or it can now be calculated by means of the ratio just established. The latter method for field work is far simpler and more expedient. The soil sample taken in the field for soil moisture determination, although ample for duplicate measurements of the moisture equivalent, is usually not large enough for a single wilting coefficient determination. Moreover, the period of time required for wilting coefficient determinations, combined with the uncertainty which accompanies all physiological work when duplication is impossible, makes this determination less expedient and the results in such cases less reliable than those derived from the moisture equivalent by the use of the ratio here established.

The relationship established between the wilting coefficient and the moisture equivalent led us to believe that a similar relationship might be found for some of the other physical measurements of soil moisture retentivity. We have accordingly made similar comparisons of the wilting coefficient with the hygroscopic coefficient, the moisture holding capacity, and the soil texture, as expressed by mechanical analysis. The last mentioned determination does not measure moisture retentivity, but it does measure certain properties of the soil which determine the moisture retentivity to a large extent. We will now consider the results of these comparisons.

THE RELATION OF THE WILTING COEFFICIENT TO THE HYGROSCOPIC COEFFICIENT

When a dry soil is placed in a saturated atmosphere, it will absorb water vapor until a condition of approximate equilibrium is attained. The moisture content of a soil under such conditions is known as the hygroscopic coefficient of that soil.

The determination of the hygroscopic coefficient, unless carried out with special precautions, is not very exact. It is influenced by variation in temperature and by any departure from a condition of complete saturation of the surrounding air.[9] The time element is also an important factor, since the soil absorbs water very slowly, particularly near the point of equilibrium. In fact, equilibrium would not be theoretically obtained until the interstitial spaces of the soil were practically filled with water. The method thus has certain inherent disadvantages which are not encountered in moisture equivalent determinations.

The hygroscopic moisture determinations given in this paper were carried out in a double-walled ice chest kept in a subterranean room, where the temperature was approximately 20 C°.[10] The bottom of the chest was covered with water and the zinc walls were lined with blotting paper which was kept saturated.

A comparison of the hygroscopic coefficient and the wilting coefficient for a number of soils is given in the accompanying table (table III). The soils used are the same as those employed in the preceding experiments, being arranged in order of increasing moisture equivalents.

The hygroscopic determinations given in the table are the mean of duplicate measurements. The determinations range from 0.5 per cent in sand to 13.2 per cent in clay loam. The corresponding wilting coefficients have been discussed in connection with the preceding table.

The ratio of the hygroscopic coefficient to the wilting coefficient is given for each soil in the last column of the table. The mean of this ratio is 0.68, with a probable error of ± 0.012. We have,

[9] HILGARD, E. W., Soils. 1906. p. 196.

[10] Determinations by J. W. McLANE.

then, in this ratio a second method of determining the wilting coefficient, when the hygroscopic coefficient is known, as follows:

$$\frac{\text{Hygroscopic coefficient}}{0.68 \pm 0.012} = \text{wilting coefficient.}$$

HEINRICH[11] determined the non-available moisture in six types of soil, using the wilting points of corn and oats as indicators. He

TABLE III

THE RELATION OF THE WILTING COEFFICIENT TO THE HYGROSCOPIC COEFFICIENT IN SOILS RANGING FROM SAND TO CLAY

No.	Soil type	Hygroscopic coefficient	Wilting coefficient		Ratio of hygro. coefficient to wilting coefficient
			No. dets.	Average	
7	Coarse sand	0.5	11	0.9	0.556
2	Fine sand	1.5	16	2.6	0.577
8	Fine sand	2.3	3	3.3	0.698
9	Fine sand	2.3	2	3.6	0.639
3	Sandy loam	3.5	9	4.8	0.729
10	Sandy loam	4.4	3	6.3	0.699
4	Fine sandy loam	6.5	13	9.7	0.670
12	Loam	7.8	3	10.3	0.757
A	Sandy loam	6.3	1	9.9	0.636
B	Fine sandy loam	6.6	1	10.8	0.611
C	Fine sandy loam	7.5	1	11.6	0.646
5	Loam	9.8	12	13.9	0.705
D	Loam	9.6	1	15.2	0.631
13	Clay loam	11.8	2	14.6	0.808
14	Clay loam	13.2	4	16.2	0.815
E	Clay loam	11.2	1	16.5	0.679
6	Clay loam	11.4	16	16.3	0.700

Mean... 0.680

Probable error of mean......... ±0.012

also measured the hygroscopic coefficient of each soil used in his experiments. We have computed from his measurements the mean ratio of the hygroscopic coefficient to the wilting coefficient, together with the probable error of the mean, obtaining the value 0.696±0.03, as compared with the ratio 0.68±0.01 obtained from our experiments. While HEINRICH's determinations show more variation than our own, the ratio obtained from his results agrees within the limits of his probable error with the ratio obtained in

[11] HEINRICH, R., *l.c.* 28–32.

our experiments. A single determination by ALWAY,[12] in which barley plants were used, gave a ratio of 0.65.

In the absence of a more definite relationship between non-available moisture and the hygroscopic coefficient, ALWAY[13] has advocated deducting the hygroscopic coefficient from the field soil moisture determinations as a basis for comparing the available moisture in soils. Our measurements, however, show that the wilting coefficient is about 1.47 times the hygroscopic coefficient, so that very misleading results may be obtained from this approximation, particularly when the moisture supply is limited. For example, consider two soils containing respectively 14.7 per cent and 20 per cent of water and each having a hygroscopic coefficient of 10 per cent. Under these conditions all the water in the first soil is practically non-available for growth, while the second contains over 5 per cent of available moisture. Simply deducting the hygroscopic coefficient would lead to the erroneous conclusion that both soils contained considerable available moisture.

It is important in this connection to distinguish clearly between the hygroscopic coefficient, as used above, and the hygroscopic water content, which is simply the water content of "air-dry" soil. The latter term has recently been used by DUGGAR,[14] who, in discussing HEINRICH's results as given by CAMERON and GALLAGHER,[15] says: "It will be noticed that so soon as the amount of water in ordinary soil becomes about three times the hygroscopic water content, it begins to assume physiological importance." The water content of air-dried soil may vary according to atmospheric conditions from practically zero in the case of some sun-dried desert soils to the hygroscopic coefficient

[12] ALWAY, F. J., Soil studies in dry land regions. Bur. Plant Industry, Bull. 130. 17–42. 1908.

[13] ALWAY, F. J., Studies of soil moisture in the "Great Plains" region. Jour. Agric. Sci. 2:334. 1908.

[14] DUGGAR, B. M., Plant physiology. 1911, pp. 56, 57.

[15] CAMERON, F. K., and GALLAGHER, F. E., Bureau of Soils, U.S. Dept. Agric., Bull. 50, pp. 57, 58. An error occurs in CAMERON and GALLAGHER's paper in connection with HEINRICH's results. They give his determinations on air-dried soils, but state that these determinations were made after exposing the soils to a saturated atmosphere for a week.

when exposed in a saturated atmosphere. There is consequently nothing definite or reproducible about such determinations, unless the conditions under which the measurements were made are also known, and any ratio derived from such measurements is likely to give misleading results when applied to other determinations.

THE RELATION OF THE WILTING COEFFICIENT TO THE SATURATION COEFFICIENT AND THE "MOISTURE HOLDING CAPACITY" OF SOILS

The saturation water content or the saturation coefficient is the percentage of water held in the soil when all interstitial space is filled with water. The "moisture holding capacity" is the percentage of water a soil can retain in opposition to the force of gravity when free drainage is provided. This is dependent upon the height of the soil column employed, diminishing as the height of the column is increased.[16] When the soil column is made very short, for example 1 cm. in height, the two determinations are practically identical. Both are greatly influenced by the packing and the granulation of the soil, so that determinations are subject to wide variation in the hands of different observers.

In the accompanying table (table IV) the wilting coefficients of a series[17] of soils are compared with the moisture holding capacity. Following HILGARD,[18] the latter determinations were made with a soil column 1 cm. in height, with free drainage.

The moisture holding capacity of the soils used in the comparison ranged from 23 to 71 per cent. In this case the ratio between the moisture holding capacity and the wilting coefficient is not constant. However, an approximately constant relationship is obtained if the moisture holding capacity is first reduced by 21. The ratio of the moisture holding capacity less 21 to the wilting coefficient is shown in the last column of the table. The mean ratio for the 15 soils

[16] HILGARD, E. W., and LOUGHRIDGE, R. H., Rept. Calif. Sta. 1892–94.

BRIGGS, L. J., Mechanics of soil moisture. U.S. Dept. Agric., Div. of Soils, Bull. 10. 1897.

[17] In this work it was not possible to secure samples of all the soils used in the preceding experiments.

[18] HILGARD, E. W., Soils. 1906, p. 209.

examined is 2.90±0.06. The relationship between the wilting coefficient and the moisture holding capacity is then:

$$\frac{\text{Moisture holding capacity}-21}{2.9\pm0.06}=\text{wilting coefficient.}$$

TABLE IV

RELATIONS OF THE WILTING COEFFICIENT TO THE MOISTURE HOLDING CAPACITY

No.	Soil type	Moisture holding capacity percentage	Wilting coefficient percentage	Ratio of moisture holding capacity −21 to wilting coefficient
7	Coarse sand	23.2	0.9	2.44
2	Fine sand	29.9	2.6	3.40
8	Fine sand	28.5	3.3	2.27
9	Fine sand	31.4	3.6	2.84
F	Sandy loam	44.9	8.3	2.88
G	Sandy loam	50.1	9.5	3.06
H	Loam	55.9	11.0	3.17
I	Loam	58.6	11.6	3.24
J	Loam	59.8	11.7	3.30
86	Clay loam	54.2	13.8	2.40
K	Clay loam	58.2	14.7	2.52
L	Clay loam	63.2	14.9	2.83
M	Clay loam	71.3	15.0	3.35
N	Clay loam	67.2	15.7	2.94
O	Clay loam	69.5	16.7	2.90

Mean..........2.90

Probable error of mean ratio ....±0.06

RELATION OF WILTING COEFFICIENT TO SOIL TEXTURE AS EXPRESSED BY MECHANICAL ANALYSIS

Soil texture has been more extensively used than any other physical property for the quantitative description of soils, and unfortunately it has been one of the most difficult to interpret from the standpoint of moisture retentiveness. Texture is quantitatively expressed by means of the mechanical analysis, which shows the composition of the soil when the particles are separated into groups according to size. The accuracy with which the texture of the soil can be expressed by this means is dependent upon the number of groups into which the particles are separated. But the difficulty of securing a complete separation of the finer particles into the desired groups places a practical limit upon the number of groups, which is usually limited to seven.[19]

[19] BRIGGS, L. J., MARTIN, O. F., and PEARCE, J. R., The centrifugal method of mechanical soil analysis. U.S. Dept. Agric., Bur. Soils, Bull. 24. 1904. p. 33.

The use of mechanical analysis as a basis for determining the moisture retentiveness of a soil is further complicated by the fact that soils having a high clay content will show great differences in the amount of colloidal material, which greatly affects the moisture retentiveness. Furthermore, the particles constituting a given group may lie much nearer one limit of the group than the other, so that a given group does not always have the same properties. We are then led to conclude that the particles constituting a given group in the mechanical analysis do not always have the same moisture retentiveness per unit mass, or that their specific retentivity when measured alone is modified to some extent by admixture with particles from other groups.

BRIGGS and McLANE,[20] using the method of least squares, have established a relationship between the mechanical composition and the moisture equivalent, based upon data covering 104 soil types. The resulting probable error of the coefficients in the relationship established is ± 1.7 per cent.[21] In attempting the correlation of the mechanical composition with the non-available moisture, we have used the same *relative* values for the sand, silt, and clay coefficients that were obtained by BRIGGS and McLANE in their moisture equivalent correlation. The actual values of the coefficients were adjusted to give the best calculated values for the wilting coefficient, but the same proportion among the coefficients was maintained. The formula used was as follows:

$$0.01 \text{ sands} + 0.12 \text{ silt} + 0.57 \text{ clay} = \text{wilting coefficient.}$$

In this formula the "sands" refer to the percentage of particles ranging from 2 to 0.05 mm. in diameter, the "silt" to particles from 0.05 to 0.005 mm. in diameter, and the "clay" to particles smaller than 0.005 mm. in diameter. In the accompanying table[22] (table V) is given the mechanical composition of each of the soil types, the computed value of the wilting coefficient as determined by the above formula, the observed value of the wilting coefficient,

[20] BRIGGS, L. J., and McLANE, J. W., *l.c.*, 18.

[21] This value should not be confused with the probable error of a single determination, as given by BRIGGS and McLANE.

[22] We are indebted to the Bureau of Soils for the mechanical analysis. No mechanical analyses were available for samples nos. 6 and 14.

and the residuals or the difference between the observed and the computed values.

TABLE V

COMPARISON OF THE OBSERVED WILTING COEFFICIENT WITH THAT FOUND BY COMPUTATION FROM THE MECHANICAL ANALYSIS

No.	Soil type	Coarse sand mm. 1–0.25 percentage	Fine sand mm. 0.25–0.05 percentage	Silt mm. 0.05–0.005 percentage	Clay mm. 0.005–0 percentage	Wilting coefficient: Computed percentage	Wilting coefficient: Observed percentage	Residuals	Ratio of obsvd. to comp.
7....	Coarse sand	60.4	37.1	0.8	1.6	1.8	0.9	+0.9	0.50
2....	Fine sand	28.2	64.4	4.7	3.9	3.1	2.6	+0.5	0.84
8....	Fine sand	35.4	55.1	4.8	4.5	3.6	3.3	+0.3	0.92
9....	Fine sand	29.9	56.7	5.0	8.2	3.8	3.6	+0.2	0.95
3....	Sandy loam	33.1	50.0	8.6	7.5	4.9	4.8	+0.1	0.98
4....	Fine sandy loam	2.8	59.8	30.2	6.9	10.3	9.7	+0.7	0.94
12....	Loam	3.4	55.5	21.8	19.1	9.5	10.3	−0.8	1.08
A.....	Sandy loam	32.4	28.8	26.7	11.8	9.9	9.9	0.0	1.00
B.....	Fine sandy loam	15.8	42.4	28.7	12.9	10.7	10.8	−0.1	1.01
C.....	Fine sandy loam	19.2	35.6	30.6	14.7	11.4	11.6	−0.2	1.02
5....	Loam	2.0	48.8	37.7	12.3	13.5	13.9	−0.4	1.03
D....	Loam	3.6	35.2	41.4	14.4	14.6	15.2	−0.6	1.04
14....	Clay loam	5.1	27.0	35.2	32.5	14.5	16.2	−1.7	1.12
E.....	Clay loam	3.2	43.7	45.1	17.1	16.0	16.5	−0.5	1.03
6....	Clay loam	4.4	20.5	52.6	22.0	16.6	16.3	+0.3	0.98

The ratio of the observed to the computed value of the wilting coefficient is also given in the last column of the table in order to provide a basis of comparison as regards accuracy with the other physical measurements. The mean ratio[23] is 1.00, with a probable error of ±0.025. This large probable error is due mainly to soil no. 1, which has a departure no greater than some of the other soils, but which on account of its very small wilting coefficient gives a ratio which is widely divergent from the rest of the series. The formula for computing the wilting coefficient, when affected with its probable error, then becomes:

$$\frac{0.01 \text{ sands} + 0.12 \text{ silt} + 0.57 \text{ clay}}{1 \pm 0.025} = \text{wilting coefficient.}$$

[23] In determining the values of the sand, silt, and clay coefficients so as to give a mean ratio equal to unity, soil no. 1 was disregarded, since a better general agreement was obtained in this way. This is virtually what would have happened if the method of least squares had been applied to the experimental data. In all calculations of probable error, however, this soil has been included with the rest.

COMPARISON OF THE ACCURACY OF THE INDIRECT METHODS FOR DETERMINING THE WILTING COEFFICIENT

Since the numerical value of the ratio used in calculating the wilting coefficient by indirect methods varies considerably according to the method employed, it is necessary for purposes of comparison to express the probable error in each case as a percentage of the ratio which it affects. This comparison is given in the accompanying table (table VI).

TABLE VI

SHOWING THE COMPARATIVE ACCURACY OF THE RATIOS USED IN THE INDIRECT METHODS FOR DETERMINING THE WILTING COEFFICIENT

Method	Ratio	Probable error of mean ratio	
		Absolute value	Percentage of ratio
Moisture equivalent........	1.84	±0.013	±0.7
Hygroscopic coefficient.....	0.68	±0.012	±1.8
Moisture holding capacity ..	2.90	±0.06	±2.1
Mechanical analysis	1.00	±0.025	±2.5

The probable error of the mean ratio shows the degree of uncertainty that is attached to the value given for the ratio. That is to say, if the moisture equivalent series were repeated, the chances are even that the mean ratio would fall between 1.827 and 1.853. In other words, in a soil having an observed moisture equivalent of 18.4 per cent, the chances are even that in so far as the accuracy of the ratio is concerned the wilting coefficient lies between 9.93 and 10.07 per cent. This corresponds to an uncertainty of ±0.7 per cent in the value of the wilting coefficient calculated by means of the ratio 1.84, as shown in the last column of the table.

The last column of the table shows the probable error of the mean ratio expressed as a percentage of the ratio itself. This affords at once a means of comparing the accuracy of the different ratios. It will be seen that the probable error arising from the uncertainty of the ratio in calculating the wilting coefficient by the moisture equivalent method is about 0.7 per cent; by the hygroscopic coefficient method 1.8 per cent, or over twice as great; by the moisture-holding capacity method 2.1 per cent, or three times as great; and by the mechanical analysis method 2.5 per cent, or nearly four times as great.

It should be recognized clearly that the formulae which have been deduced will not necessarily give the correct calculated value of the wilting coefficient within the limits of the probable error of the ratio. The uncertainty regarding the value of the observed quantity (moisture equivalent, hygroscopic coefficient, etc.) enters into the calculation of the wilting coefficient for any particular soil, in addition to the uncertainty of the ratio. According to the formulae, a linear relation exists between the observed quantity and the wilting coefficient in each case, and the observed departures are attributed to accidental experimental errors. If this is true, then the probable error of the calculated wilting coefficient for a given soil can be made to approach the probable error of the ratio as a limit simply by increasing the accuracy and number of the determinations of the observed quantity.

The probable error of a single determination of the wilting coefficients in our experiments is given below for each method, expressed in per cent of the wilting coefficient.

Moisture equivalent method, ± 2.9 per cent
Hygroscopic coefficient method, ± 7.1 per cent
Moisture holding capacity method, ± 8.3 per cent
Mechanical analysis method, ± 10.0 per cent

These errors are not to be applied to any other determinations, since they represent simply the degree of accuracy attained in our particular experiments. If the number of physical measurements made upon each soil had been increased, the error would have been reduced.

FORMULAE SHOWING RELATIONSHIPS BETWEEN PHYSIOLOGICAL AND PHYSICAL MEASUREMENTS OF MOISTURE RETENTIVITY

For convenience in reference, the formulae for determining the wilting coefficient of a given soil by indirect methods are here presented in collected form, together with the probable error.

$$\text{Wilting coefficient} = \frac{\text{moisture equivalent}}{1.84(1 \pm 0.007)}$$

$$\text{Wilting coefficient} = \frac{\text{hygroscopic coefficient}}{0.68(1 \pm 0.018)}$$

$$\text{Wilting coefficient} = \frac{\text{moisture holding capacity} - 21}{2.90(1 \pm 0.021)}$$

$$\text{Wilting coefficient} = \frac{0.01 \text{ sands} + 0.12 \text{ silt} + 0.57 \text{ clay}}{1 \pm 0.025}$$

SUBSIDIARY FORMULAE

We have also included the subsidiary formulae which follow as the result of the interrelationships established. The probable error has been omitted, since its determination from the formulae would always include the experimental errors of the wilting coefficient determination, due to the fact that the physical measurements are not directly compared.

For the determination of moisture equivalent[24]

Moisture equivalent = wilting coefficient × 1.84
Moisture equivalent = hygroscopic coefficient × 2.71
Moisture equivalent = (moisture holding capacity − 21) × 0.635
Moisture equivalent = 0.02 sand + 0.22 silt + 1.05 clay

For the determination of the hygroscopic coefficient

Hygroscopic coefficient = wilting coefficient × 0.68
Hygroscopic coefficient = moisture equivalent × 0.37
Hygroscopic coefficient = (moisture holding capacity − 21) × 0.234
Hygroscopic coefficient = 0.007 sand + 0.082 silt + 0.39 clay

For the determination of the moisture holding capacity

Moisture holding capacity = (wilting coefficient × 2.9) + 21
Moisture holding capacity = (moisture equivalent × 1.57) + 21
Moisture holding capacity = (hygroscopic coefficient × 4.26) + 21
Moisture holding capacity = (0.03 sand + 0.35 silt + 1.65 clay) + 21

These formulae establish for the first time a relationship between the various physical and physiological measurements of moisture retentivity, and while the coefficients may be modified as a result of further investigation, it is believed that the equations will prove of practical value in the study of the relationship of the plant to soil moisture, both in the field and laboratory.

For the determinations of the maximum available moisture

The maximum moisture available for growth in any soil is represented by the difference between the moisture holding capacity and the wilting coefficient. It is possible, therefore, to express the *maximum* amount of available moisture that a soil is capable of holding in terms of the relationships given above. It should be recalled that the moisture-holding capacity determinations, upon

[24] These equations refer to moisture equivalent determinations made with a centrifugal force equal to 1000 grams and should not be confused with the equation given by BRIGGS and MCLANE (*l.c.*) in which a force of 3000 grams was employed.

which the relationships are based, were made with a soil column 1 cm. in height. The amount therefore is far in excess of that found in drained soils under field conditions. The relationships are expressed in the following formulae:

$$\text{Maximum available moisture} = (\text{wilting coefficient} \times 1.9) + 21$$
$$\text{Maximum available moisture} = \text{moisture equivalent} + 21$$
$$\text{Maximum available moisture} = (\text{hygroscopic coefficient} \times 2.8) + 21$$
$$\text{Maximum available moisture} = (0.02\ \text{sand} + 0.23\ \text{silt} + 1.08\ \text{clay}) + 21$$
$$\text{Maximum available moisture} = (\text{moisture holding capacity} \times 0.65) + 7$$

The formulae show that difference in the maximum amount of available moisture that two soils are capable of holding is equal to the difference in their moisture equivalents; to 1.9 times the difference of their wilting coefficients; and to 2.8 times the difference of their hygroscopic coefficients.

Summary

An investigation was made to determine whether the wilting coefficient of a soil can be computed from physical measurements of its moisture retentivity. A comparison of the wilting coefficient is made with the moisture equivalent, the hygroscopic coefficient, the moisture-holding capacity, and the mechanical analysis, for a series of soils ranging from sand to clay. From this comparison, a series of linear relationships is established, as expressed in the following equations, which form a means of computing the wilting coefficient when direct determinations are not feasible.

$$\text{Wilting coefficient} = \frac{\text{moisture equivalent}}{1.84\ (1 \pm 0.007)}$$

$$\text{Wilting coefficient} = \frac{\text{hygroscopic coefficient}}{0.68(1 \pm 0.018)}$$

$$\text{Wilting coefficient} = \frac{\text{moisture holding capacity} - 21}{2.90(1 \pm 0.021)}$$

$$\text{Wilting coefficient} = \frac{0.01\ \text{sand} + 0.12\ \text{silt} + 0.57\ \text{clay}}{1 + 0.025}$$

The second term of the quantity within the brackets shows the probable error of the relationship in each case, and constitutes a measure of the relative accuracy of the different methods.

U.S. Department of Agriculture
Bureau of Plant Industry
Washington, D.C.

AN ISOLATED PRAIRIE GROVE AND ITS PHYTOGEOGRAPHICAL SIGNIFICANCE[1]

HENRY ALLAN GLEASON

(WITH TWO FIGURES)

Probably less study has been given in recent times to the relation of prairie and forest than to any other general phytogeographical problem in the central states. Some of the large number of questions still awaiting satisfactory solution were briefly stated in a former paper,[2] and in the following pages some evidence bearing on one of them is given and some conclusions of a more general nature are drawn. The present paper is not so much a description of modern conditions as an attempt to explain by existing distribution certain historical features of the relation of forest and prairie in central Illinois. It is probable that the conclusions drawn from the local area apply equally well to many other portions of the eastern extension of the Prairie Province.

Early histories and maps show that the prairies of central Illinois were not continuous, but occupied chiefly the higher ground between the drainage systems. The latter were bordered in their lower courses by forests, which occupied the floodplain and bluffs and extended out a short distance on the uplands. The sources of the streams were usually in the prairie, and their margins were occupied by prairie vegetation for the first few miles. Scattered about on the prairie were a few isolated groves, far removed from the larger bodies of forest along the water courses. These groves were important to the Indians and early settlers as landmarks and camping grounds, and at a later period formed centers from which the settlement of the prairie proceeded. Bur Oak Grove is an example of such an isolated area of forest. It is situated in the east-central part of Champaign County, on the east side of the

[1] Contribution no. 123 from the Botanical Laboratory of the University of Michigan.

[2] Some unsolved problems of the prairies. Bull. Torr. Bot. Club 36:265–271. 1909.

Chicago and Eastern Illinois Railway, not far from the village of Royal. There were several other isolated groves in the county, most of which have been entirely destroyed by cultivation. Of these, Bur Oak Grove is the largest and the most significant phytogeographically. The remaining forest areas of the county are along the Sangamon and Kaskaskia rivers, and Salt Fork of the Vermillion River. The last two rise in the county, and the upper five to ten miles of their course is in the prairie.

The present length of Bur Oak Grove is about three miles from northeast to southwest, and its width about one mile. It is certain that it was originally somewhat longer, and it probably had a greater average width. Its outline is and has always been very irregular. In recent years cultivation has broken it up into many small detached portions. There is no easily accessible map showing the location of the grove in detail. The Urbana sheet of the Topographic Survey just misses the grove on the west. Just southwest of Bur Oak Grove, however, are two or three other detached groves of similar topography which appear on the map. These areas are indicated in green near Glover station. The peculiar topography associated with these groves is scarcely shown, even on a map with contour intervals at ten feet.

The most striking physical feature of the grove is its peculiar surface topography. Surrounded on all sides by level prairie country, it is sharply and conspicuously distinguished by its irregular surface, which consists of alternating elevations and depressions. The elevations are of about the same height, and the intervening depressions are also of a very uniform depth. The width of the depressions varies from a hundred feet to a quarter of a mile; their length from a few hundred feet to half a mile, or perhaps more; and their depth is usually about ten feet. Their shape accordingly varies from almost circular to linear, and those of the latter shape frequently resemble abandoned channels of some water course. They lie in every conceivable position, and may branch or anastomose in any way. As a result of the general irregularity, the intervening elevated ground may consist of circular islands, extended surfaces, or long and narrow, straight, curved, or branching ridges. For convenience, they are here always

referred to as ridges, irrespective of their shape, while the depressions are called sloughs, after the general usage of the region. The slope from ridge to slough is always gentle, never exceeding and seldom reaching 10°. No attempt will be made to explain the origin of this peculiar topography, except to suggest that it may be in some way connected with or caused by the glacier which deposited the conspicuous moraine a few miles farther north.

These sloughs received all the surface drainage from the ridges, and were originally filled through most of the year with standing water. During the spring rains they overflowed at the lowest point in their margins into neighboring sloughs, and in this way the whole area was converted into a network of ponds. During the summer the water was lost by underground drainage and evaporation, until by October some of the sloughs were entirely dry.

These conditions have greatly restricted agriculture, and it is to them that the grove owes its preservation. With the increasing value of land, tile has been laid, ditches dug, and most of the sloughs reclaimed. In them the soil is black and deep and is generally planted to corn. Others are left in pasture, although they support a better growth of weeds than of grass. A few are so deep that they cannot be profitably drained, and are still occupied by permanent ponds. Probably half a dozen of these ponds are left, and they now constitute the only natural bodies of permanent standing water in the county. Although the soil on the ridges is not so black or so deep as on the surrounding prairies, a part of the forest which covered them has been cleared, and the staple crops are grown. The rest of the forest is used for permanent pasture.

The forest cover of the ridges shows a considerable variation in specific composition from south to north. Near the south end the forest is open, the trees are comparatively small, and there is scarcely any deposit of leaf mold (fig 1). The prevailing trees are *Quercus imbricaria*, *Q. velutina*, *Carya ovata*, *C. cordiformis*, with occasional trees of *Juglans nigra*. The actual proportion of these species varies widely. *Quercus imbricaria* is usually most abundant, but there are some small areas in which *Carya ovata* is dominant. The trees now seldom exceed a foot in diameter, but the present forest is almost

entirely second growth. Old stumps may be seen which are two feet or more in diameter, and a few veteran trees are still standing. The forest is open enough to permit the growth of blue grass, and the continual pasturage has resulted in the destruction of nearly all the native herbaceous species. The chief native plants remaining are *Muhlenbergia Schreberi*, *Geum canadense*, *Sanicula canadensis*, and *Veronica virginica*, and occasionally a small thicket of *Corylus americana*. *Verbascum Thapsus* and some other introduced weeds are frequent. At the margin of the forest there are

FIG. 1.—Forest at south end of the grove; *Quercus imbricaria* is here the dominant tree.—Photograph by ARTHUR G. VESTAL.

in some places small thickets of *Pyrus coronaria*, *Crataegus* sp., *Prunus americana*, and *Viburnum prunifolium*.

Near the middle of the grove, from south to north, several other species of trees are common. Most important among these in size and number is the bur oak, *Quercus macrocarpa*, which gave the grove its name. A few large trees, three to four feet in diameter, serve to give some idea of the dimensions of the original stand. There are also numerous trees of *Juglans nigra*, *Ulmus fulva*, *Celtis occidentalis*, *Prunus serotina*, and *Gleditsia triacanthos*. The four species of the south end of the grove are still present, although naturally relatively less abundant. Near the margin of this portion

of the forest, and in the more open places within it, avevectent shrubs are abundant. The commoner ones are *Smilax hispida*, *Menispermum canadense*, *Crataegus Crus-galli*, *Crataegus* sp., *Evonymus atropurpureus*, *Celastrus scandens*, *Psedera quinquefolia*, *Vitis vulpina*, *Zanthoxylum americanum*, *Sambucus canadensis*, and *Viburnum prunifolium*. Where the forest is too dense to permit the growth of blue grass, many of the original herbaceous species still persist. Among them the following were listed: *Dioscorea villosa*, *Parietaria pennsylvanica*, *Polygonum virginianum*, *Phytolacca decandra*, *Silene stellata*, *Anemone virginiana*, *Aquilegia canadensis*, *Heuchera hispida*, *Agrimonia mollis*, *Rosa setigera*, *Lespedeza frutescens*, *Amphicarpa monoica*, *Polygala Senega* var. *latifolia*, *Viola* sp., *Sanicula canadensis*, *Seymeria macrophylla*, *Triosteum perfoliatum*, *Campanula americana*, *Helianthus strumosus*, *Verbesina helianthoides*, *Aster Drummondii*, *Lactuca villosa*.

In the northernmost part of the grove the four trees of the southern end still persist, but are much less abundant than other species. *Quercus macrocarpa*, *Juglans nigra*, *Celtis occidentalis*, and *Ulmus fulva* are common; *Gleditsia triacanthos* grows 60–80 feet high; there are a few trees of *Prunus serotina*, *Ulmus americana*, and *Populus grandidentata*, and, most notable from an ecological viewpoint, *Quercus rubra* and *Tilia americana* appear. At the northeast corner of the grove *Quercus rubra* is the dominant species, with the largest living trees about three feet in diameter. In this part of the grove there is a conspicuous deposit of leaf mold on the ground, and the forest cover produces a denser shade. As a result, the herbaceous vegetation is decidedly mesophytic and includes many species which are typically members of the climax forest association. Among these are *Arisaema triphyllum*, *Allium tricoccum*, *Trillium recurvatum*, *Smilax ecirrhata*, *Pilea pumila*, *Ranunculus abortivus*, *Podophyllum peltatum*, *Impatiens pallida*, *I. biflora*, *Circaea lutetiana*, *Cryptotaenia canadensis*, *Phlox divaricata*, *Pentstemon laevigatus* var. *Digitalis*, *Phryma Leptostachya*, *Galium concinnum*, and *Eupatorium urticaefolium*. Avevectent shrubs are not so common as in the middle portion of the forest, and blue grass grows only in partial clearings.

Direct observation shows at once that the forest is always con-

fined to the ridges, and measurement with a Locke level or alidade not only confirms this idea, but shows that the lower and outer margin of the forest follows a definite contour line, so that the forest margins on all sides of a slough lie at exactly the same level. This contour line is approximately two feet above the maximum level of standing water in the slough. The forest margins on opposite sides of a ridge will be at the same level if the sloughs are connected, but otherwise they may differ slightly in elevation. Within the forest, the various species of trees, with one exception, show no relation to the elevation, but are equally abundant on the sides and top of the ridges. The exception is formed by *Gleditsia triacanthos*, which regularly chooses the lower outer margin, nearest the sloughs and in the wettest soil. This feature has been observed also in other isolated groves in the county. The shrubs, if present at all, seem to prefer the margin of the forest, but in this case the controlling factor is probably light instead of water.

Some very definite and sharply marked zones of vegetation occur between the forest and the center of the pastured sloughs. The first is a zone of blue grass which extends out beyond the forest margin to a distance depending on the steepness of the slope, and down to the former level of maximum high water in the slough. Because of the continual pasturage it contains few secondary species. The second zone is composed of a very dense and rank growth of *Ambrosia artemisiifolia*, with scattered plants of *Vernonia fasciculata*, *Eupatorium serotinum*, *Bidens cernua*, *B. aristosa*, *Polygonum acre*, and *Verbena hastata*. It is probable that the dominance of *Ambrosia*, and the relative infrequency of other species, is caused by pasturing, in which certain species are selected for food, and others with rank smell or taste are avoided by the cattle and horses. This idea is substantiated by the different composition of the same zone around a slough in an unpastured field. In this tangle of weeds may be found a few scattered plants of some typical swamp hydrophytes, such as *Iris versicolor*, *Mimulus ringens*, *Scirpus fluviatilis*, and *Penthorum sedoides*. These are naturally most abundant in the deepest part of the slough, but show no present relation to contour lines (fig. 2).

Around those sloughs which contain permanent ponds a better

idea of the zonation may be gained. In such places the second zone contains some *Ambrosia*, but the dominant species are various grasses and sedges, especially *Leersia oryzoides* and *Glyceria nervata*. *Bidens aristosa* is common, and there are numerous scattered plants of the species mentioned before. Within and below this zone is a third, in which the dominant plants are again grasses and sedges, and in which *Iris versicolor*, *Mimulus ringens*, *Penthorum sedoides*, *Lippia lanceolata*, *Asclepias incarnata*, *Lobelia siphilitica*, and other

Every plant listed as living in the sloughs is by preference a prairie species. Throughout the series not one typical plant of the forest has been seen. Such common and characteristic plants of floodplain swamps and oxbows as *Hibiscus militaris*, *Cephalanthus occidentalis*, and *Ambrosia trifida* are entirely absent. The oldest settlers say that there never were either white or yellow water lilies. On the contrary, they state that the margins of the sloughs were occupied by "slough grass" (*Spartina Michauxiana*) tall enough to hide a man on horseback. So it is obvious that these were prairie sloughs rather than forest swamps, and that the vegetation must have been entirely distinct from and independent of the forest vegetation of the ridges. A reconstruction of the whole grove would present a series of prairie sloughs, with grassy vegetation, alternating with the series of forested ridges. An interpretation of the phytogeographical significance of this condition will now follow.

The forest evidently indicates three stages in a successional series, beginning with the oaks and hickories at the south, passing through the bur oak stage at the center, and ending with the red oak stage near the north end. This succession is the usual one for central Illinois, and is caused, at least in part, by the gradual accumulation of humus and decrease in light. There are many other places in the state where the same series may be observed under different ecological circumstances. It is especially typical of the succession of forests on uplands along a stream, and is met with in traversing such a forest at right angles to the course of the stream. The presence of a few trees of basswood at the extreme north end may be construed to indicate the approaching development of the hard maple-basswood type of forest, the highest type found in central Illinois. Along stream courses this normally follows the red oak stage, and is located accordingly nearer the stream. The chief difference between the forests of a river system and Bur Oak Grove lies not in their structure, but in the fact that the former are connected with a general forest system extending down the ri[illegible] to an indefinite distance, while in the latter the grove is entir[illegible] isolated from other bodies of forest. The ori[illegible] forests o[illegible] river system can be explained by the g[illegible] ntinu[illegible]

immigration of plants along a river highway. In the isolated grove it must be explained by a connection, no longer existent, with an older forest source, or by the sporadic development of the forest following a discontinuous migration across the prairie.

Considering the second alternative, it might be possible for the various successional stages to develop centrifugally about a small forest center, the first stage occupying an outer ring, while the following ones appeared toward the middle. This does not seem possible here, because the arrangement is so obviously unilateral, with the later stages in the succession progressively farther toward the northeast, while there is no obvious difference in the environment between the two ends of the grove, which might lead to the readier development of the red oak stage at one end. Also, in every other forest examined in central Illinois, in which oaks are the dominant trees, it has been possible to show a definite connection with some other body of forest, from which continuous migration might have taken place. In other words, oaks, with their heavy immobile seeds, do not seem able to cross tracts of prairie to a more favorable habitat, but must migrate in an uninterrupted path. There are isolated groves in Champaign County, whose structure suggests that they are the result of a discontinuous migration, but no oaks occur in them.

Considering now the first alternative, the development of Bur Oak Grove through immigration along the small streams of the vicinity is precluded for several reasons. First, their valleys are too shallow to afford the necessary physiographic diversity which always accompanies a mesophytic type of forest in central Illinois. Secondly, they all flow to the south, while in Bur Oak Grove the more mature forest type is at the north. Thirdly, they would have served as well or better for the immigration of hydrophytes than for upland species, while, as has been shown, the hydrophytic vegetation of the grove consists entirely of prairie species. The arrangement of species in the grove is exactly similar to the unilateral arrangement paralleling water courses in central Illinois. The whole grove has the appearance, and conveys the impression, of being the margin, now the only part remaining, of some extensive body of forest immigrating from the northeast, the location

of the more advanced stages, toward the southwest, the present location of the pioneer black oak and shingle oak. Of all the possibilities, development of the grove by continuous immigration from the northeast seems the only plausible explanation, and is accepted as the correct conclusion.

This idea postulates the existence in the past of a large tract of forest farther to the northeast, from which immigration into the grove took place. A few miles beyond the grove a moraine extends from northwest to southeast, perpendicular to the general direction of the forest migration, and beyond the moraine and parallel to it is the Vermillion River, bordered with a narrow belt of forest. The original source of Bur Oak Grove must be looked for at the river or along the moraine.

Several reasons lead to the belief that the moraine was the site of the ancient forest from which Bur Oak Grove was populated. In the first place, the scanty forests along the river are entirely incommensurate in size, and the distance is too great. Secondly, moraines in northeastern Illinois and parts of central Illinois are regularly forested, and other moraines in Champaign County have even now small groves upon them. Most important of all, various moraines in central Illinois have upon them forest relics which point indubitably toward a former forest covering. Thickets of hazel, an immobile forest plant not seriously injured by forest fires, are known from several places. On the moraine north of Bur Oak Grove, *Erythronium albidum*, *Trillium recurvatum*, and *Claytonia virginica* occur. These forest mesophytes produce seed in this region so seldom and propagate by vegetative means so regularly, that they cannot be considered recent invaders from the forest upon the prairie. They die to the ground in the summer, before the season of prairie fires, and their persistence on the prairie is probably due to this habit, together with their ability to withstand exposure to the full sunlight. Because of these three reasons, it seems probable that the moraine was originally covered with a forest of some luxuriance, and that from it as a center invasion of the surrounding prairies took place. Other moraines must have been similarly forested, so that in some prehistoric time a vastly larger proportion of the state was covered with forest than at pres-

ent. The entire absence of forest relics over most of the prairie makes it extremely improbable that the entire surface of the county was ever forested. The level till plains between the stream systems and the moraines were probably prairie even at the time of greatest forest advance. The immigration of the forest was restricted to the two lines of greatest physiographic diversity, the stream valleys and the moraines.

We must now account for the removal of this large body of forest from the moraine, and for the persistence of the small remainder in a few outlying tracts like the one at Bur Oak Grove. Examination of the conditions in the grove will suggest the reason, which is substantiated by other observations elsewhere in the county.

Along the western margin of the grove some of the ridges are still forested, while others are under cultivation. Examination of the vegetation along the roadsides on the cultivated ridges shows on some of them such typically forest plants as *Aster Drummondii*, *Silene stellata*, *Hedeoma pulegioides*, and others. It is evident from the flora that these ridges were originally forested also. On some other ridges these species are entirely absent, and the roadside vegetation consists of typically prairie species, as *Andropogon furcatus*, *Sorghastrum nutans*, *Panicum Scribnerianum*, *Silphium integrifolium*, *Petalostemum violaceum*, and *Parthenium integrifolium*. Evidently these ridges were originally prairie. By this method of observation of the relic plants, the exact boundaries of the grove can be determined. In this way it becomes evident that, in every case, those ridges which are or were forested are protected on the west by a conspicuous slough, while the prairie ridges extend west without interruption out upon the open prairie. Since the forested part of the grove is exclusively on the ridges, it is clear that the whole forest was protected on the west side by a series of sloughs. The prevailing winds are also from the west, and prairie fires driven to the eastward by a west wind were unable to cross the slough into the forest. It may be concluded, accordingly, that prairie fires were the chief and probably the only agent in the removal of the forest from the moraines and other places where it was not properly protected by a water barrier. The grove

at Bur Oak was benefited by a peculiar and unusual topography, and was virtually the only portion of an extensive forest system to be spared.

The origin of the prairie as a type of vegetation cannot, however, be referred to prairie fires as a cause, as was frequently supposed by early authors and occasionally even in recent years. A prairie fire presupposes a prairie, and in prairie fires we have merely one factor which has been of assistance in the maintenance or extension of the prairie in its struggle against forest invasion. In the last half century, since the cessation of prairie fires, the forests have again begun an advance into the prairie, but, as is well known, their route is chiefly up the streams, and the migration is limited to a comparatively small number of mobile species. Because of increasing cultivation, this migration is very irregular and can never lead to any serious modification in the vegetation of the region.

In conclusion, the conditions in Bur Oak Grove serve to indicate the last three periods in the vegetational history of the state:

1. Period of forest advance, leading to a great development of forests in areas of physiographic diversity.

2. Period of prairie fires, following the advent of man and leading to the restriction of the forest to protected areas and the corresponding extension of the prairie.

3. Period of civilization and the virtual cessation of the struggle between forest and prairie.

UNIVERSITY OF MICHIGAN

SOME FEATURES IN THE ANATOMY OF THE SAPINDALES[1]

RUTH HOLDEN

(WITH PLATES II AND III)

In studying the phylogeny of plants, there are certain general principles upon which all conclusions are based. One of these deals with the retention of ancestral characteristics. A striking example of this is afforded by the anatomy of the cycads. The vegetative stem of these forms always has exclusively centrifugal metaxylem, but in the leaf petiole, the metaxylem is predominately centripetal, with only a slight development in a centrifugal direction. Centripetal wood structure is, of course, the more primitive, and its appearance in the leaf petiole of the Cycadales serves to relate them to their extinct Cycadofilicean ancestors, where centripetal wood was present in the stem. Similar bundles with centripetal wood are present also in the reproductive axes of certain Cycadales.[2]

Another well known seat of primitive conditions is the root, good examples of which are furnished by the Abietineae. The first and older subtribe, the Pineae, is characterized by the invariable presence of resin canals in the normal wood of both root and stem, while in the more modern subtribe, the Abietae, resin canals are generally absent in the normal wood of the stem. Resin canals do occur, in all four genera of the Abietae, in the center of the primary wood of the root.[3]

Recent investigations have shown that ancestral conditions may be recalled as a result of wounding. For example, these resin canals, present in the roots of the Abietae, are present invariably

[1] Contributions from the Phanerogamic Laboratories of Harvard University, no. 42.

[2] SCOTT, D. H., The anatomical characters presented by the peduncle of Cycadaceae. Ann. Botany 11:399–419. *pls. 20, 21.* 1897.

[3] JEFFREY, E. C., The comparative anatomy and phylogeny of the Coniferales. II. The Abietineae. Mem. Boston Soc. Nat. Hist. 6:1–37. *pls. 1–7.* 1904.

in the wood formed immediately after injury. Anatomical evidence thus shows that there are present in the leaf, petiole, root, and wounded tissue of gymnosperms, structures quite unlike those normally occurring in the stem; and paleobotanical evidence shows that these are primitive features, retained in certain restricted localities long after they have disappeared elsewhere. Instance after instance could be cited where these two lines of evidence, anatomical and paleobotanical, reinforce each other in the gymnosperms. In the angiosperms, however, no such checking up is possible as yet, because of the comparative scantiness of fossil material. Here the anatomical principles worked out from a study of gymnosperms have to be relied on exclusively in tracing their phylogeny.

Another principle of comparative anatomy is that simple conditions are not necessarily to be interpreted as primitive. This is well recognized by zöologists, who regard tunicates as vertebrates which, in losing almost entirely their vertebrate characteristics, have reverted to a simpler ancestral organization, and as degenerate rather than primitive. Or, on the botanical side, *Abies* has as simple normal wood as any known; there are only two types of elements present, tracheids and parenchyma, transverse and longitudinal. In the roots of all species, however, there are specialized resin canals, surrounded by parenchymatous epithelial tissue; these are present also in the reproductive axes of certain species. Another complication is present in the wounded root of at least one species,[4] where above and below the parenchymatous ray cells there are rows of tracheidal cells, forming ray tracheids like those of *Pinus*. Applying the principles of comparative anatomy, it is evident that *Abies* is descended from forms which had both resin canals and ray tracheids, and its simplicity of wood structure is not primitive, but a result of degeneracy.

It is the purpose of this paper to present the conditions found in certain of the Sapindales, and then to interpret them in accordance with these principles. For this purpose, four representative genera were chosen; *Aesculus*, *Acer*, *Sapindus*, and *Staphylea*.

[4] THOMPSON, W. P. The origin of ray tracheids in the Coniferae. BOT. GAZ. 50:101–116. 1910.

Fig. 1 shows a transverse section of the wood of *Aesculus Hippocastanum* L., and fig. 2 a tangential section of the same. From these it is possible to make out the main features of the wood. Woods may be grouped into three classes, depending on the distribution of parenchyma: (1) a primitive type with only terminal parenchyma on the "face of the summer wood"; (2) a more advanced type with parenchyma scattered throughout the year's growth, that is "diffuse"; and (3) the highest type with parenchyma only around the vessels, or "vasicentric." *Aesculus* belongs to the third of these groups; furthermore, its parenchyma is chiefly on the tangential wall of the vessels. The mechanical elements of the wood also exhibit a high degree of specialization, in that they are all transformed to libriform fibers, with characteristically thick walls, and narrow, obliquely elongated simple pits. The vessels are scattered throughout the year's growth, giving the "diffuse porous effect." The vessels have pits on the side walls closely crowded together, but never fused, end walls with porous perforations, and tertially spiral thickenings on their inner walls. Thus in having vasicentric parenchyma, libriform fibers, and vessels with porous perforations, *Aesculus* has the wood structures characteristic of the highest dicots, but the rays present a peculiarly simple condition. They are always of the linear, uniseriate type, like those of many of the gymnosperms.

Figs. 1 and 2 represent *Aesculus Hippocastanum*, but the wood is practically indistinguishable from that of its near relative *Aesculus glabra* Willd., as well as other species of the genus, and this description applies equally to all.

Fig. 3 represents a tangential section of *Acer saccharum* Marsh. The wood is "diffuse porous" like that of *Aesculus*, and the parenchyma is likewise vasicentric, but less abundant, and instead of being on the tangential wall, it is on the radial wall. The libriform fibers are heavier than those of *Aesculus*, especially those immediately around the vessels, which are very thick walled, while those in the intervals are larger and thinner walled. The vessels are very similar to those of *Aesculus*, having porous perforations on the end walls, densely crowded pits on the side walls, and well marked tertiary thickenings. The rays, however, are strikingly

different. These are a few of the uniseriate variety, but the majority are multiseriate.

Figs. 4 and 5 represent transverse and tangential sections of the wood of *Sapindus* sp. Like the two genera described, the wood is "diffuse porous"; the parenchyma is vasicentric and abundant. The fibers are characterized by delicate cross partitions of cellulose, constituting the so-called "septate fibers." Though some of the vessels are small, the majority are large, serving at once to separate *Sapindus* from the other members of the Sapindales. They have porous perforations and spiral thickenings; the side walls in some places have closely crowded pits, but in other places there is a decided tendency toward fusing into rows of slitlike bordered pits. The rays of *Sapindus* are multiseriate, much like those of *Acer*.

Fig. 6 represents another member of the Sapindales, *Staphylea trifolia* L. Here the wood parenchyma is vasicentric, and usually on the radial side of the vessels. The wood elements are not as specialized as in the other genera; instead of being libriform or septate fibers, they are fiber tracheids, with thinner walls and conspicuously bordered pits. The vessels have both porous and scalariform perforations; the pits on the side walls are sometimes unfused like *Acer* and *Aesculus*, but are more often united to form large slit like openings. *Staphylea* is the only one of the four genera examined in which there are no spiral markings on the inner walls of the vessels. The rays range from 1 to 10 cells wide. These broad rays cause a local "dipping in" of the annual ring, like that in *Quercus*.

Having considered the general characteristics of these four members of the Sapindales, the question arises as to which is the most primitive and which the most advanced. Disregarding the evidence furnished by the ray, *Staphylea*, with its scalariform perforations and fiber tracheids, seem to be the lowest; but taking the ray structure into consideration, *Aesculus* seems to be the lowest. Thus the question narrows down to which is the more primitive for the Sapindales, uniseriate or multiseriate rays.

In this connection it is interesting to note the work of EAMES of this laboratory on the genus *Quercus*.[5] He found the rays of

[5] EAMES, A. J., On the origin of the broad ray in *Quercus*. BOT. GAZ. 49:161–167. *pls. 8, 9.* 1910.

Quercus to be of two sorts, linear or uniseriate, and broad or compound. In investigating the relative primitiveness of these two types, he examined a fossil oak from the Miocene. Here he found the same two sorts of ray, uniseriate and broad, but the broad rays, instead of being homogeneous masses of parenchyma, were composed of smaller rays, separated from each other by fibers, or by fibers and wood parenchyma. This condition lead to the suspicion that broad rays of living oaks might be derived from the aggregation and fusion of small rays. Accordingly, he examined seedlings of a number of oaks, and found such to be the case. Seedlings of black oaks show, near the pith, a ray structure like that of the miocene oak, with a gradual, progressive fusion until a single, homogeneous, compound ray is formed. Seedlings of white oaks show a still more primitive condition. In some, for the first 15 or 20 years, only uniseriate rays appear, which generally fuse into compound rays. Thus both anatomical and paleobotanical evidence point to the conclusion that for *Quercus* uniseriate rays are primitive, and that the large rays are formed by a process of fusion.

This conclusion is further strengthened by a consideration of conditions found in wounded oaks. BAILEY[6] of this laboratory investigated a number of species of this genus, and found that in every case, after a severe wound, a broad ray breaks up into a number of uniseriate or small rays, a clear case of traumatic reversion.

This compounding process BAILEY has examined in a number of genera of the Betulaceae and Fagaceae, with similar results. For example, in *Alnus*[7] he finds all types, from exclusively uniseriate rays in *A. acuminata* H.B.K. to completely fused aggregate or compound rays in *A. rhombifolia* Nutt.

The uniseriate rays of *Aesculus*, therefore, are open to two interpretations; they may be primitive like those of white oak seedlings, in which case *Aesculus* has a very low type of wood structure; or they may be the result of reversion, in which case *Aesculus* is

[6] BAILEY, I. W., Reversionary characters of traumatic oak woods. BOT. GAZ. 50:374–380. *pls. 11, 12.* 1910.

[7] BAILEY, I. W., Relation of the leaf trace to the origin and development of compound rays in the dicotyledons. Ann. Botany (ined.).

descended from ancestors which had multiseriate rays like those of *Acer*, *Sapindus*, and *Staphylea*. In determining this point, one must rely on the principles of comparative anatomy worked out for the gymnosperms, and investigate the parts of a plant which are most tenacious of ancestral characteristics, namely, leaf petiole, reproductive axis, and root.

Figs. 7 and 8 represent transverse sections of the leaf petiole of *Aesculus Hippocastanum;* fig. 9 a tangential section of the same, and in all three the multiseriate type of ray is conspicuous. When a leaf petiole leaves the branch, there is no one woody cylinder, but instead, 20–30 small vascular strands. Most of these strands arrange themselves in the form of a circle, and fuse to form a siphonostele, but certain ones, perhaps 5–10, instead of taking up a peripheral position, remain in the center. These medullary bundles are at first collateral in structure, but soon the xylem begins to grow around the phloem, until they become amphivasal, forming bundles such as are found typically in monocot rhizomes. This siphonostelic condition with medullary bundles is found throughout the length of the petiole, up to the bases of the leaflets. Then the cylinder is broken again into a large number of vascular strands, which in the bases of the leaflets repeat the process carried on in the base of the petiole. Some take up a peripheral position and form a siphonostele, while one or two remain in the pith as medullary bundles. These medullary bundles, however, are always collateral, never amphivasal. The important point is that throughout the prevailing type of ray is multiseriate. This is equally true of the separate strands as they leave the main branch, of the woody tissue of the siphonostele of both petiole and leaflet, and of the medullary bundles of both petiole and leaflet. Usually the rays as they leave the pith are biseriate or triseriate; sometimes they remain so to the cambium, but usually they become reduced to a uniseriate condition. Another peculiar condition seen in tangential section is the longitudinal elongation of the ray cells.

It is one of the principles of plant anatomy that the leaf trace is tenacious of ancestral conditions, and it is interesting to note that in the case of *Aesculus* these primitive conditions are retained,

not only in the leaf trace, but also in the wood of the axis immediately around the leaf trace. Fig. 10 represents an outgoing foliar bundle; subtending it, there is a mass of ray parenchyma forming a true multiseriate ray. Often in the case of numerous small bundles going into the petiole, this mass of tissue extends all the way from one bundle to the next.

These photographs are all of *Aesculus Hippocastanum*, but the conditions of *Aesculus glabra* are essentially the same, except that under the leaf trace there is seldom as much parenchyma as here shown.

Fig. 11 is a tangential view of the wood of a root, showing an outgoing rootlet and the tissue immediately under it. The conditions are very much as in the branch, each rootlet trace being subtended by numerous multiseriate rays. Usually, however, this condition is not so pronounced in the root as in the branch.

Fig. 12 is a tangential section of a floral axis, showing the conditions immediately below an outgoing flower stalk or peduncle. The rays are characteristically biseriate, and extend sometimes a long distance below the trace. Often above the trace they are broader than below, but they never extend as far. The woody tissue is as a whole poorly developed, except at the end of each flower stalk, where it becomes much thicker. Just below the end, there are 5 or 6 traces going out simultaneously, each of which has a small number of multiseriate rays below it.

Three of the recognized primitive localities have thus been shown to have well marked multiseriate rays, and wounded wood was examined for the same structures. None were found, either because the injury was not sufficiently severe, or because the degeneracy of *Aesculus* has gone too far to be recalled traumatically.

Aesculus then presents a condition just the reverse of that found in *Quercus*. The former has uniseriate rays normally, with multiseriate rays persisting in primitive localities; the latter has compound rays normally, with uniseriate rays in primitive localities. Accordingly, multiseriate rays are primitive for the Sapindales, and *Aesculus*, instead of being the most primitive of the Sapindales, on the basis of ray structure, is really advanced, its simplicity being due to degeneracy.

Summary and conclusions

1. Investigations of the anatomy of living and fossil gymnosperms have proved certain general principles. One is that primitive structures occur in the fibrovascular bundles of the leaf petiole, the root, and the reproductive axis, and sometimes revert in wounded wood.

2. Of the Sapindales investigated, three show multiseriate rays normally: *Acer*, *Sapindus*, and *Staphylea;* the fourth, *Aesculus*, shows uniseriate rays normally, but multiseriate rays in the leaf petiole, root, and reproductive axis.

3. Applying the general principles enumerated above, it is evident that the multiseriate type of ray is primitive for the Sapindales, and that *Aesculus* is a degenerate member. Accordingly, the Sapindales belong high in any systematic arrangement of dicotyledonous woods.

In conclusion, I wish to express to Dr. E. C. JEFFREY my sincere thanks for his suggestions and advice during the course of this investigation.

RADCLIFFE COLLEGE
CAMBRIDGE, MASS.

EXPLANATION OF PLATES II AND III

PLATE II

FIG. 1.—*Aesculus Hippocastanum;* transverse section of wood, showing uniseriate rays; ×80.

FIG. 2.—The same: tangential section of wood, showing similar rays; ×80.

FIG. 3.—*Acer saccharum:* tangential section of wood, showing multiseriate rays; ×80.

FIG. 4.—*Sapindus* sp.: transverse section of wood, showing multiseriate rays; ×80.

FIG. 5.—The same: tangential section of wood, showing similar rays; ×80.

FIG. 6.—*Staphylea trifolia:* tangential section of wood, showing multiseriate rays; ×80.

PLATE III

FIG. 7.—*Aesculus Hippocastanum:* transverse section of leaf petiole, showing multiseriate rays; ×180.

FIG. 8.—The same: transverse section of leaf petiole in another region, showing similar rays; ×180.

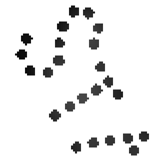
FIG. 9.—The same: tangential section of leaf petiole, showing similar rays; ×80.

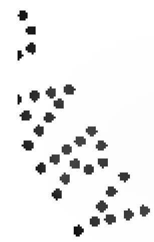
FIG. 10.—The same: tangential section of branch, showing outgoing foliar bundle with subtending multiseriate rays; ×80.

FIG. 11.—The same: tangential section of root, showing outgoing rootlet with subtending multiseriate rays; ×80.

FIG. 12.—The same: tangential section of reproductive axis, showing multiseriate rays below outgoing flower stalk; ×80.

HOLDEN on SAPINDALES





HOLDEN on SAPINDALES

THE MORPHOLOGY OF THE SEED OF BUCKWHEAT

NEIL E. STEVENS

(WITH EIGHT FIGURES)

The Polygonaceae have been several times referred to in recent literature as being characterized by the production of seeds having an abundant perisperm (JOHNSON **7**, p. 337; COULTER and CHAMBERLAIN **3**, p. 179). This character has been taken by JOHNSON as an indication of rather close relationship between the Polygonaceae and the Piperaceae, in which family he has observed a perisperm. These statements as to the seed of the Polygonaceae are apparently based on the work of HARZ (**4**, p. 1072), who includes this family among the "Curvembryonaten," which he characterizes as "Eine grosse natürliche Gruppe . . . . alle ausgezeichnet durch den Besitz eines reichlichen mehlhaltigen Perisperms und eines meist peripherisch gelagerten Embryo." HARZ (p. 1102) figures and describes in considerable detail the structure of the buckwheat seed, and evidently considers the entire storage region as perisperm. He also states that the same condition occurs in species of *Rumex*. KRAEMER (**9**), to be sure, speaks of the Polygonaceae as having an endosperm, but does not discuss the morphology of the seed.

A careful study of the seed of *Fagopyrum esculentum* has convinced the writer that in this genus at least no perisperm is present at maturity. The material used in this study was collected during the summer of 1910 and fixed in Juel's fluid (JUEL **8**). Microtome sections were used exclusively. These were cut rather thick, usually about 12μ, and stained with Delafield's haematoxylin.

The early development of the embryo appears to be typical in every respect. In fact, up to the stage at which the cotyledons begin to be differentiated, the embryo corresponds almost cell for cell with the often figured *Capsella Bursa-pastoris*, in which, however, the suspensor is considerably longer.

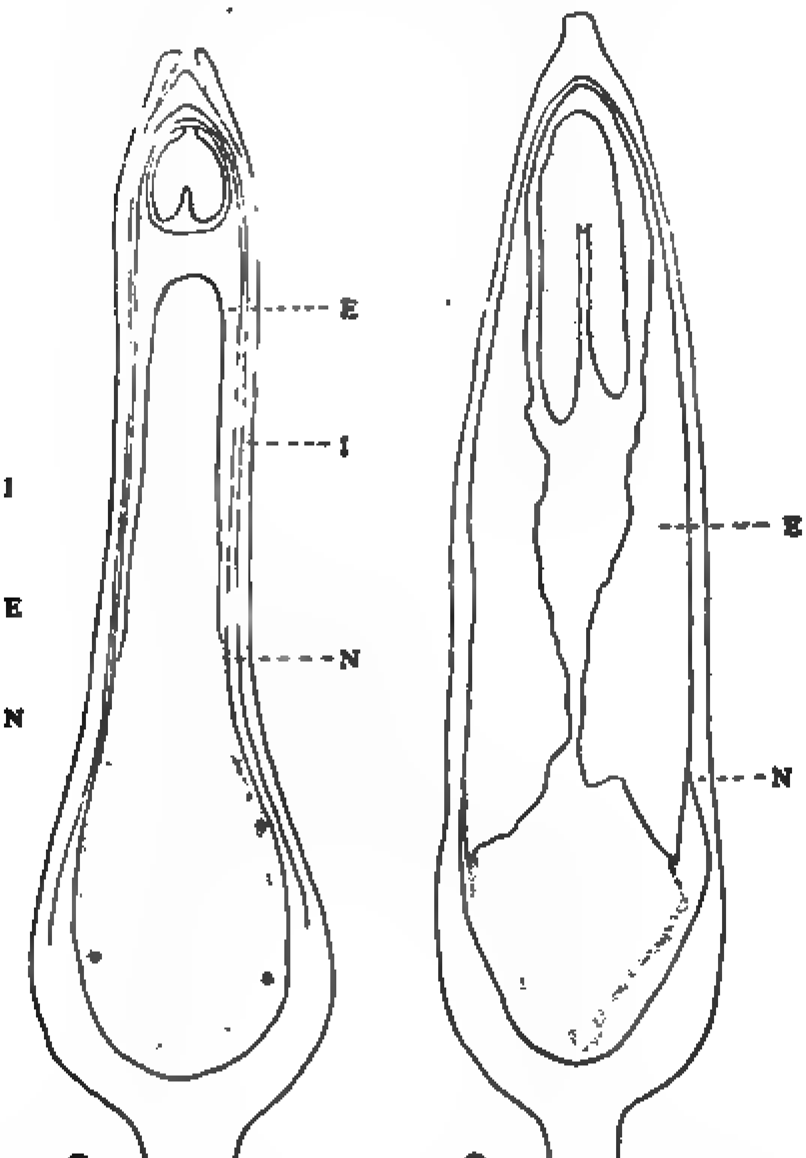
Free nuclear division apparently begins in the embryo sac soon after fertilization, and by the time the embryo has reached the

, the endosperm contains at least 32 nuclei, heral layer of cytoplasm. The nucellus at ' in the lower half of the ovulary cavity. A differing markedly from the rest, extends

I

E

N



2 3

tudinal median section of ovule, showing the embryo in idosperm in the free nuclear condition; the cells of the nd the inner layer of the integument are outlined in the ig. 2, similar section about the time the cotyledons are bryo; the upper portion of the endosperm has become have appeared in the lower portion; $\times 33$; fig. 3, later opment of the embryo and of the cellular portion of the nents; *N*, nucellus; *E*, endosperm.

is outer layer becomes differentiated some on, and consists of closely packed, regular the possession of rather dense granular nce of a vacuole.

Growth and nuclear division are most rapid in the upper portion of the endosperm, that is, in the region between the growing embryo and the degenerating nucellar tissue. Cell formation begins in this region about the time the cotyledons first appear in the embryo. The cells arise centripetally and with great regularity. Apparently only a single nucleus is included in each cell, and there is no evidence of nuclear fusions. Cell formation gradually extends both above and below the region where it originates, and soon a marked differentiation is evident in the endosperm. At the stage shown in fig. 2, cell formation has progressed till a portion of the endosperm, some 8 or 10 cells thick, extends entirely across, just below the embryo. Above, around the developing embryo, the endosperm consists of only a single layer of cells; while below the thickest region, the endosperm becomes thinner, consisting toward the bottom of fewer and fewer layers of cells; till at the base, for at least a third of its length, the endosperm does not become divided into cells at all, but consists merely of a layer of cytoplasm with scattered nuclei, enclosing a large sap cavity.

This marked differentiation of the endosperm into two regions, one of which shows no cell formation whatever, suggested the chambered embryo sacs described by HOFMEISTER (**5**, p. 185), STRASBURGER (**11**, p. 111), and others, in which the first division of the primary endosperm nucleus is followed by the formation of a cross wall, dividing the embryo sac into two chambers, in only one of which the endosperm is developed. Careful study of early stages makes it seem certain, however, that no such cross wall occurs in the embryo sac of the buckwheat.

Soon after the stage just described, a secondary differentiation becomes evident in the cellular portion of the endosperm; the outer layer taking on the appearance and function of a cambium layer, which cuts off cells only on the inner side. A similar condition has been figured by CHAMBERLAIN (**2**, p. 344) in the developing endosperm of *Dioon edule*. These "cambium" cells divide rapidly; and the continued growth of the cells thus formed forces the wall of the ovary outward, and causes the more central portion of the endosperm to extend downward toward the base of the ovule. No further development occurs in the lower portion of the original

embryo sac (fig. 3). At the same time, the embryo is developing at the expense of the inner portion of the endosperm, so that the cells of the endosperm at this stage differ considerably in appearance. The "cambium" cells and the cells adjacent to them are thin-walled and closely packed. Nearer the center the cells become larger and vacuolate, some of them containing a considerable amount of starch; their walls also become slightly thicker, and the continued growth of the ovule pulls them apart, so that intercellular spaces of considerable size occur. Of the cells nearest the embryo only the crushed and distorted walls remain (fig. 4, *E*).

Nearly all the nucellar tissue has been destroyed by this time. The differentiated outer layer, however, persists in an actively growing condition, differing from the earlier stages only in that the cells have elongated and show, in some instances, small vacuoles (fig. 4, *N*). This outer layer of the nucellus is apparently composed of two quite different regions, which grade insensibly into each other. The upper portion, around the micropyle, consists of a plate of cells which apparently undergo no change after the time of fertilization. The cells of the lower portion continue to grow actively with very little if any cell division. They increase somewhat in thickness, and to a very marked degree in surface extent, keeping pace with the growth of the young seed. As the embryo nears maturity, these cells become more and more coarsely vacuolate (fig. 5, *N*), and in the mature seed only the crushed remains of this layer are present (fig. 6, *N*).

The fact that this layer persists in an actively growing condition till the growth of the endosperm is practically complete, together with the dense granular nature of the cell contents, suggests that it has a nutritive function, the "nutritive jacket" of COULTER and CHAMBERLAIN (**3**, p. 103). Similar layers, presumably nutritive in function, have been observed in numerous instances. Usually this "nutritive jacket" is derived from the integument; in one case however, ***Armeria plantaginea***, BILLINGS (**1**, p. 278) describes such a layer, which he calls a "tapetum," as derived from the outer portion of the nucellus. In ***Erodium gruinosum*** BILLINGS finds this "tapetum" two layers thick, one layer of cells being derived from the integument and one from the nucellus. He describes a

"tapetum" derived from the integument in numerous genera, notably *Linum*, *Geranium*, *Primula*, *Phacelia*, and *Lobelia*.

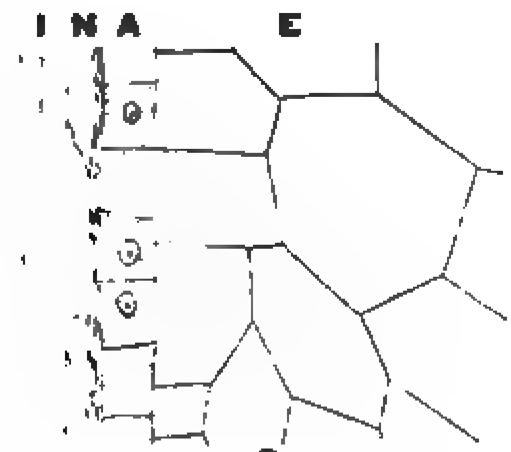
LLOYD (**10**, p. 103) has recently shown that in the date the integument serves to some extent to distribute nutritive material to the developing endosperm. In the buckwheat, however, the integu-

I N E

4

I N E

5



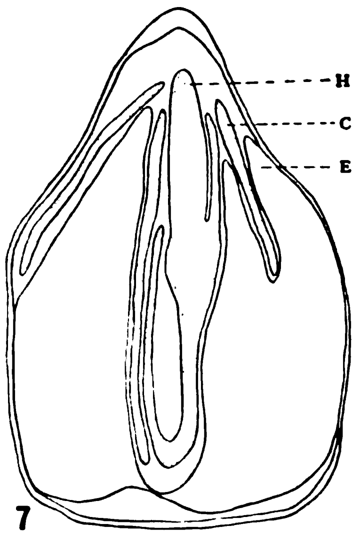
6

FIGS. 4–6.—Fig. 4, portion of longitudinal section at about the stage shown in fig. 3; only the outer layer of the nucellus, the "nutritive jacket," remains functional; the endosperm shows an outer layer of embryonic cells and a more central region of large vacuolate cells; some of the larger cells contain starch grains; ×260; fig. 5, later stage; the cells of the nutritive jacket have become vacuolate; ×260; fig. 6, mature grain; the nucellus remains merely as a thin region of crushed cells; the outer layer of endosperm cells is differentiated as an aleuron layer, the other endosperm cells are crowded with starch; ×260; *I*, integuments; *N*, nucellus; *E*, endosperm; *A*, aleuron layer.

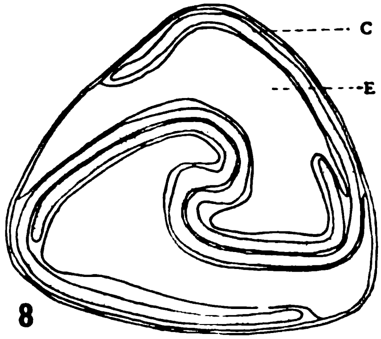
ments seem to have no part in this process. In fact, they undergo very little differentiation, but remain throughout the growth of the seed as thin, rather uniform structures, each consisting of but two layers of cells. As there are no vessels present in the ovule which might accomplish this work, it seems entirely probable that the outer layer of the nucellus functions for the transfer of nutritive

substances from the chalazal region to the growing endosperm. Such an explanation might account for the fact that the endosperm develops fastest in the upper portion, the broken down cells of the nucellus forming, lower down, an effective barrier to the passage of food material.

In its later development the embryo becomes remarkably unsymmetrical, and as the cotyledons increase in size they become considerably curved. At maturity the cotyledons are broad and rather thin; and since the blade on one side of the midrib is twice as wide as on the other and the midribs lie together, one cotyledon on each side extends considerably beyond the other. In a cross section of the seed they present the appearance of a much exaggerated letter S (fig. 8, *C*). This peculiarly unsymmetrical nature of the embryo makes the endosperm exceedingly irregular.



7



8

FIGS. 7, 8.—Fig. 7, longitudinal median section of mature seed; ×15; fig. 8, transverse section of mature seed, below the hypocotyl; ×15; the parts of the embryo are shaded; *E*, endosperm; *C*, cotyledons; *H*, hypocotyl.

Shortly before the seed is mature, a further differentiation takes place in the endosperm. The cambium layer, after it has ceased cutting off starch storing cells, divides further by anticlinal walls; thus forming a continuous layer of short regular cells, filled in the mature seed with dense granular contents, but containing no starch. This is an aleuron layer, the "eiweisshaltige Zellen" of HARZ (fig. 6, *A*). Except for this single aleuron layer, the irregular endosperm consists of large,

closely packed cells, filled with starch. In its development the cellular portion has been crowded well down toward the base of the ovule. Even in the mature fruit, however, a space containing the remains of the undeveloped basal portion of the embryo sac is always present in the chalazal region (fig. 7).

The absence of a perisperm in the buckwheat does not of course exclude the possibility of its occurrence in other members of the Polygonaceae. That such a variation is sometimes found in nearly related genera is shown by the work of HUMPHREY (6) on the Scitaminales. In this order HUMPHREY found a progressive series of stages in the development of the endosperm. The Musaceae have a large starch bearing endosperm, in the Zingiberaceae and Cannaceae the endosperm is thin and contains only aleuron, while in the Marantaceae it is apparently not present in the mature seed. Variation occurs, as HUMPHREY shows, even within a single family. Among the Musaceae, *Heliconia* shows a distinct, though rather thin, starch bearing perisperm, while in *Strelitzia* only a thin layer of nucellar tissue showing no cellular structure remains in the mature seed. It is interesting to note that in the latter genus the massive endosperm never wholly fills the cavity of the seed, a condition comparable to that noted by the writer in *Fagopyrum*.

YALE UNIVERSITY

LITERATURE CITED

1. BILLINGS, FREDERICK H., Beiträge zur Kenntnis der Samenentwickelung. Flora 88:253–318. 1901.
2. CHAMBERLAIN, C. J., The ovule and female gametophyte of *Dioon*. BOT. GAZ. 42:321–358. 1906.
3. COULTER, J. M., and CHAMBERLAIN, C. J., Morphology of angiosperms. New York. 1903.
4. HARZ, C. O., Landwirthschaftliche Samenkunde. Berlin. 1885.
5. HOFMEISTER, W., Neuere Beobachtungen über Embryobildung der Phanerogamen. Jahrb. Wiss. Bot. 1:82–188. 1858.
6. HUMPHREY, JAMES E., The development of the seed in the Scitamineae. Ann. Botany 10:1–37. 1896.
7. JOHNSON, D. S., On the development of certain Piperaceae. BOT. GAZ. 34:321–338. 1902.
8. JUEL, H. O., Die Tetradenteilungen bei *Taraxacum* und anderen Cichoriaceen. Kgl. Svenska Vet. Akad. 39⁴:1–20. 1905.

9. Kraemer, Henry, A text-book of botany and pharmacognosy. Ed. 4. Philadelphia. 1910.

10. Lloyd, F. E., Development and nutrition of the embryo, seed, and carpel in the date, *Phoenix Dactylifera* L. From the 21st Ann. Rep. Missouri Bot. Garden. 103–164. 1910.

11. Strasburger, E., Zellbildung und Zelltheilung. Ed. 3. Jena. 1880.

BRIEFER ARTICLES

DEVELOPMENT OF THE ZYGOSPORE OF RHIZOPUS NIGRICANS

(PRELIMINARY NOTICE)

In growing *Rhizopus nigricans* for laboratory use, there was produced an unusual abundance of zygospores. This supply of material, and the increasing interest in the Mucorales in general, made it seem worth while to investigate the development of the zygospore of this species. Since completion of the investigation is temporarily delayed, the results so far obtained seem to be of sufficient interest to warrant the publication of a preliminary account.

There is a streaming of protoplasm with nuclei into the young suspensors, followed by a denser accumulation at the contact ends of the suspensors.

Before the gametangia are cut off, there appears a difference in the density and staining capacity of the protoplasm of the two suspensors, and this difference persists until the zygospore is mature.

The walls, cutting off the gametangia from each other, may not be formed simultaneously, and in each wall there is left a central pore. The wall which separates the gametangia from each other often thickens considerably before disintegration, and fragments of the thickened wall may be found in quite old zygospores. In the majority of zygospores the wall breaks down before any thickening occurs. In the late stages of the zygospore there is developed by the protoplast a thick, colorless, echinate coat, from which the brown coat may be removed, leaving the zygospore intact.

The many nuclei from each gametangium increase in size after the disintegration of the wall. All the nuclei except two disintegrate, and these two nuclei are imbedded in a coenocentrum. Preparations were submitted to Professor F. L. STEVENS, and he also identified this body as being like the coenocentrum of *Albugo*. There are indications that the coenocentrum has its origin at the point of contact of the two suspensors before the gametangia are cut off; but this needs further investigation. Neither fusion nor division of the nuclei has yet been observed. It is believed, however, that the two nuclei, left in the coenocentrum, fuse. From this stage to maturity many changes occur in the appearance of

the zygospore, but their interpretation is not yet clear. The coenocentrum persists until quite late, and in the mature zygospore there are many nuclei of the same size as those in the mycelium.

Oil is diffused throughout the young zygospore, but later the oil collects in larger globules. In the mature zygospore there is usually only one globule of oil in the center, and the protoplasm, unmixed with oil, is pressed in a comparatively thin layer against the wall.

These observations are based on the examination of over 2000 zygospores, sectioned serially, and much more material must be examined before the detailed account with illustrations will appear.—FLORENCE A. McCORMICK, *The University of Chicago.*

A NEW CALIFORNIAN CEANOTHUS

Ceanothus fresnensis Dudley, sp. nov.—Low shrub, forming rounded mats, 2–4 dm. high, with stout rigid branches, young twigs tomentose: leaves opposite, oblanceolate to (and more commonly) broadly obovate, entire or usually irregularly denticulate toward the summit, coriaceous and involute, densely tomentose on both surfaces when young, glabrate above in age; petioles 1 mm. long, tomentose: umbels terminating very short branchlets; fruiting pedicels 8–12 mm. long: capsule 6 mm. high, about 5 mm. broad; horns subterminal, erect or spreading, 1 mm. long; styles very slender, divided to below the middle.

In foliage aspect this species closely resembles some forms of *Ceanothus vestitus*, but that is an erect shrub, often a meter high or more, with much smaller capsules, which are broader than long, and which have minute dorsal horns. In fruit characters it is closely akin to *Ceanothus cuneatus*, from which it differs primarily in its low habit and small tomentose, denticulate leaves.

The name, *Ceanothus fresnensis*, was proposed by the late Professor W. R. DUDLEY some ten years ago for a plant collected by HALL and CHANDLER in the southern Sierra Nevada. The label on the type specimen, which is deposited in the Dudley Herbarium of Stanford University, reads as follows: "Stevenson Mts., Pine Ridge, Fresno County, California, altitude 5300 feet, only locality seen. Growing with *C. cordulatus*." HALL and CHANDLER 407, June 1900. During the past summer I found another small colony about 100 miles north of the original station, at Confidence, Tuolumne County, where it was growing on a dry ridge at an altitude of 4000 feet in open yellow pine woods associated with *C. cordulatus* (ABRAMS 4727).—LEROY ABRAMS, *The Dudley Herbarium, Stanford University.*

CURRENT LITERATURE

BOOK REVIEWS

Heidenhain's "Plasma und Zelle"

The second part of HEIDENHAIN'S *Plasma und Zelle*[1] appeared early in 1911. While forming a part of BARDELEBEN'S *Handbuch der Anatomie des Menschen*, the section "Plasma und Zelle" is written from a remarkably broad standpoint, so that it is of general morphological and physiological interest.

In the first part,[2] issued four years ago, after a general discussion of the cell theory, the structure of the nucleus and of central bodies is taken up in detail, followed by an extensive critique of granular theories of protoplasm. Two leading tendencies give direction to the treatment of the subject matter: on the one hand, an attempt to break down the monopoly of the cell as the morphological and physiological unit; and on the other hand, more or less closely connected with this, an attempt to bring evidence for the existence of metamicroscopical units of structure, the *protomeres*. In this the author does not move in the realm of pure speculation, but is throughout concerned with arriving at conclusions establishing the existence and illuminating the nature of the metamicroscopical protomeres from a consideration of the organization and behavior of micro- and macroscopical structures. It is difficult to give in brief an adequate account of the materials and line of argument employed, and the reader is necessarily referred to the original.

The second part begins with a detailed treatment of the structure of the striated muscle, bringing together in a lucid fashion the mass of facts which has accumulated regarding this most complicated cytoplasm, doubly interesting because of the evident relation here between structure and function. A survey of this section again directs our attention to the meagerness of the data, a voluminous literature on the subject notwithstanding, regarding the histogenesis of the various structures of the muscle cell and its anomalous position with reference to information concerning the central body. It is the one conspicuous animal cell type in which even the mere presence of central bodies has not been demonstrated.

In discussing the relative solidity of various elements of the muscle cell, the author points out that the alternative *solid* or *liquid* does not put the question regarding the aggregate condition of cell constituents. He suggests

[1] HEIDENHAIN, M., Plasma und Zelle. Zweite Lief. pp. vi+604. Jena: Gustav Fischer. 1911.

[2] ———, Plasma und Zelle. Erste Abt. pp. viii+506. Jena: Gustav Fischer. 1907.

the conception of the *organized*, in which the elementary component particles maintain within certain limits definite relations to each other, although the structure as a whole may be highly plastic, as contrasted to the *fluid*.

It is to be regretted that the author did not feel warranted in giving a digest of the available data, such as they are, regarding the changes which take place in the structure of the striated muscle cell during contraction.

In connection with the discussion of the smooth muscle, the theory of short waves of contraction is developed. Whereas in the striated muscle the contraction wave has a length many times that of the muscle cell, in the smooth muscle it is but a fraction of the length of the cell. If contraction waves start simultaneously in all the fibrillae of a cell and keep step as they advance, the contraction knot of any fibrilla comes close to those of its neighbors, with a result that a more or less complete diaphragm is formed across the cell which, as it moves along, pushes the more liquid contents before it; a conception which HEIDENHAIN made use of in accounting for protoplasmic streaming in plant cells, and which has not been weakened by PFEFFER's and RHUMBLER's criticisms. The same conception is applied in a convincing manner to the movement of granules in pigment cells, and the suggestion is made that a similar situation obtains in dividing cells, resulting in the zonated appearance often observed in astrospheres. A further interesting application of the theory of short waves of contraction is made in discussing the contraction of cilia.

The section on the nervous substance brings together in an extensive but easily accessible manner the leading data on this highly complicated subject, which is of such importance to the cell theory. The author comes out unequivocally in favor of the neuron theory, a gratifying result for the adherents of this theory, especially since the standpoint of the author noted above would have made him keen to use any possible evidence against the cell theory. In the introduction a word is spoken for the importance of psychic processes as psychic processes in the economy of organisms and not as by-products of physico-chemical changes in the nerve substance. Considerable attention is given to the relation between nucleus and cytoplasm in the nerve cell. An interesting conclusion regarding the relation of the nucleus to regenerative processes in the protoplast results from the facts observed in the regeneration of a severed nerve fiber. Here, as in other known cases, repair proceeds from the nucleated portion of the cell, the other disintegrating. In the nerve fiber the cut surface may be a meter removed from the nucleus, so that a direct transportation of material from the nucleus to the region of injury is practically excluded, the action of the nucleus apparently being a dynamical one. The author also argues in favor of the "Tigroid" as a cytochromatin, an accessory chromatin developed in consequence of the huge cytoplasmic portion of the nerve cell.

A concluding chapter discusses the filar theories of protoplasmic structures and related matters.

The work contains an abundance of suggestions and information bearing

on the problems engaging the plant physiologist and morphologist. Mention should also be made of the wealth of excellent illustrations accompanying the text.—W. MARQUETTE.

The Eusporangiatae

CAMPBELL has published[3] a summary of the present knowledge concerning the morphology of the Ophioglossaceae and the Marattiaceae. His own studies of these forms have extended through twenty years, and his opportunities for observing and collecting tropical material have been unusual, so that such a summary is extremely valuable in bringing together the author's results and conclusions. The chief interest connected with this assemblage of plants is that in all probability it represents in the present flora the very ancient group which gave rise to seed plants. The main thesis of the work, however, is that Ophioglossaceae and Marattiaceae are genetically related, and that species of *Ophioglossum* are to be regarded as the most primitive forms of this assemblage, and in fact the most primitive living vascular plants. There is hardly room for difference of opinion today as to the close relationship that exists between the Ophioglossaceae and the Marattiaceae, and it is time to remove the Ophioglossaceae from their isolation as Ophioglossales, and to associate them with Marattiaceae as eusporangiate Filicales. As to the extremely primitive character of *Ophioglossum* and its relatively direct connection with the bryophytes, there is room for considerable difference of opinion.

The connection of *Ophioglossum* with bryophytes of the *Anthoceros* type is presented fully and skilfully. In embryogeny, the Eusporangiatae are characterized by the late development of the vegetative organs, as contrasted with the leptosporangiates, so that the young sporophyte is much more fully developed before it becomes independent of the gametophyte. In fact, several roots and leaves may be developed before independence, and in some cases even spores are formed before the two generations become completely separate. Moreover, the young sporophytes of *Ophioglossum* and *Anthoceros* resemble one another in appearance, with the massive foot in both cases, and the spore case of the latter represented by the cotyledon of the former. The author sees in this cotyledon, now sterile, a "pro-*Ophioglossum*" with a sporangiferous cotyledon, and with a stemless body, consisting of only leaf and root, the latter feature still being true of *O. moluccanum*. Of course the so-called "imbedded" sex organs of *Anthoceros* have long been recognized as a pteridophyte feature. The sperms of *Anthoceros* and *Ophioglossum* are regarded as perhaps the greatest obstacle, but if pteridophytes have been derived from bryophytes, that obstacle was overcome somewhere, either outside of the group or within it.

In reference to the subterranean gametophyte, which characterizes both

[3] CAMPBELL, D. H., The Eusporangiatae, the comparative morphology of the Ophioglossaceae and Marattiaceae. Carnegie Institution of Washington, Publ. no. 140. pp. vi+229. *pls. 13. figs. 192.* 1911.

Ophioglossum and *Lycopodium*, it is stated that there is "no question" that it is a secondary condition derived from such a gametophyte as that of *Marattia*, and probably through association with the symbiotic fungus. Of course it is known that the green, aerial portion of the gametophyte of certain species of *Lycopodium* is secondary, arising from the previously formed tuberous, subterranean portion, but it is conceivable that the gametophyte of *Ophioglossum* had a different origin. It is interesting to note in this connection, what may be of service to the author's view, that the gametophyte branches of some of the Anthocerotales become tuberous and subterranean, and that this habit is not unusual among liverworts.

In presenting the comparative morphology of Ophioglossaceae and Marattiaceae, the author has used the greatest variety of structures, but the conclusion as to genetic connection seems sound. In some cases the interpretations are at variance with what have come to be conventional; but, in the main, these unconventional interpretations have not so much to do with the relations of Ophioglossaceae and Marattiaceae as with the primitive character of the former among vascular plants. For example, to conclude that a short-necked archegonium is primitive as compared with a long-necked one, and that the collateral vascular strands of *Ophioglossum* are primitive and the concentric ones of the Marattiaceae replace them later, may be true for the reasons given, but it is unconventional. There seems to be no conception of the transition region as the one of vascular origins, and that the vascular systems of stem, root, and cotyledon are related to one another through it. However, since the transition region often appears to be merely a place rather than a definite structure, perhaps we have been laying too much stress upon it.

The general conclusion is that "from some form, allied to the simpler existing species of *Ophioglossum*, the whole fern series is descended"; that in this series "the leaf is the predominant organ, the stem at first being quite subordinate in importance"; that "this ancestral fern was monophyllous and the leaf at first was a sporophyll"; and that "from this central type presumably several lines diverged, of which only a few fragments exist." The details of structure and of lines of divergence are too numerous to cite; but the contribution as a whole is essential to every student of pteridophytes.—J. M. C

Cecidology

Probably the most important general work on cecidology recently published is KÜSTER's *Die Gallen der Pflanzen*.[4] The author gives a clear and concise statement of the theories and problems which confront the botanist. In the preface he calls attention to the fact that there is no book on the general subject of gall formation, and that the recent literature has demonstrated the necessity of studying both the botanical and zoological phases of the subject. He also

[4] KÜSTER, ERNEST, Die Gallen der Pflanzen, ein lehrbuch für Botaniker und Entomologen. 8vo. pp. 437. *figs. 158.* Leipzig: S. Hirzel. 1911.

states that the work does not offer a solution of the perplexing problems or attempt a natural history study of the subject.

The introduction gives a brief résumé of the history of cecidology, of the research methods in use, and of the methods used in designating galls. Chap. i contains a brief discussion of the general groups of organisms which excite the formation of cecidia, including a list of the families and genera of insects, with the number of known European and Mediterranean species as given by HOWARD. The groups of plants which excite the formation of cecidia are given as follows: Myxomycetes, Bacteriaceae, Cyanophyaceae, Algae, Fungi, and Phanerogams. Examples are given for each group, but no complete lists of genera such as are given for the insects. Chap. ii gives a brief discussion of the host plants, showing that galls are to be found in all groups from lowest to highest, but are most abundant on the flowering plants. The chapter concludes with a list of the European and Mediterranean families of angiosperms, with the number of known galls (also according to HOWARD) on each. This list contains 109 families, the largest number of galls (901) being on Fagaceae. In this connection it is interesting to note that more than 4000 species of galls occur on 10 families of dicotyledons. Chap. iii (pp. 102) gives an excellent discussion of the morphology of galls. Chap. iv gives a good but not nearly so comprehensive a discussion of the anatomy of galls. Chap. v is a very brief discussion of the chemistry of galls.

Chap. vi is a most excellent discussion of the etiology of gall formation, and should be studied by all botanists and zoologists, especially by those who still believe that all insect galls are due to chemicals injected into the host plants by the mother insects. Attention is called to the lack of proof to substantiate the various theories, the obscure nature of the subject, and the failure thus far to produce artificially such galls as are formed by natural processes. Theories past and present, with arguments for each, are clearly stated, and the susceptibility of the host plant and its parts at various stages in its life history are given careful consideration. In this connection the author refers to facultative galls, or those in which the organism, although living within various parts of the host, can produce galls on certain parts only. In this chapter he states that in his opinion an understanding of gall building can be obtained only as a result of a comparative study of plant pathology. The chapter concludes with a discussion of the correlations between host plants and galls, of variations in galls, and of abnormal galls. Chap. vii, on the biology of galls, necessarily refers to a great deal of the discussion of the preceding chapters. After discussing the fact that some organisms attack and cause galls on many species of plants, the author takes up the relationship of the life-cycle of the parasite to the life-cycle of the host plant, the problem of biological species, gall ecology, distribution, paleontology, development and life of the gall, sexual dimorphism, opening of the galls and migration of the organisms, uses and injuries, resistance and immunity of the host plants, formation and action of poisons, inquilines, parasitic and saprophytic fungi

of galls. This chapter closes with a brief but interesting discussion of the galls formed on animals.

The work is a most comprehensive presentation of the modern aspects of the general subject of cecidology. The galls themselves are the subjects of primary consideration and the gall makers secondary. The entire subject is treated from the standpoint of the botanist, and galls are grouped with reference to their own characters and not the characters of their makers. Questions of taxonomy and alternation of generations are referred to only incidentally, but these subjects are well treated in other works on cecidology which are accessible to all energetic workers. The great bulk of the work is compiled from the writings of the Germans and French, who have been the most active investigators in this field. The author might well have given a little more attention, however, to the Italian, English, and American contributions. The work is timely and will find a welcome in every modern laboratory of general botany and plant pathology. In fact, it will be indispensable for those who expect to gain a broad and thorough knowledge of modern plant pathology.—MEL. T. COOK.

A plant physiology

In his *Plant physiology with special reference to plant production*, DUGGAR[5] has deviated far from the conventional type of texts on plant physiology. Of course the principles and even the facts of plant physiology are the same whether pure or applied. The main difference, therefore, is in the facts and principles emphasized. Unusual emphasis is laid upon mineral nutrients and soil problems, and upon factors of growth significant to crop production. A number of topics, not usually found in plant physiologies, are given a place: effect of weight and size of seed upon the vigor of the plants, parthenocarpic formation in pomaceous fruits, protection of crops by insecticides and fungicides, destruction of weeds by poison, etc.; while other phases of the subject, such as tropic, tactic, and nastic movements, are given little space. The author makes much use of material appearing in experiment station bulletins, a source little used in most texts.

No science is more fundamental to agriculture than plant physiology, and yet it has had little emphasis in the agricultural colleges and experiment stations of this country. It is certainly high time that this science takes its significant position in this field of production, and DUGGAR has given a start in the right direction. The book has the virtue of being concrete and teachable to beginners, and it is possible that the author has accomplished the double aim "to consider both the student and the general reader." Any teacher of beginners in the subject will appreciate the value of the concreteness in the text.

A careful perusal of the book leaves one feeling that it is more a selection

[5] DUGGAR, B. M., Plant physiology with special reference to plant production. Rural Science Series. 8vo. pp. xv+516. New York: Macmillan Co. 1911. $1.60.

and compilation of facts from the literature than a carefully digested product of it. It is in no sense critical and even lacks organization. This, of course, is in part a necessary outcome of the concreteness, and it is possible that it is the best sort of statement in view of the aim. Very seldom does the author refer to the fundamental physics and chemistry of plant activity. No mention is made of the application of the Van't Hoff temperature law of rate of chemical reaction or of the Weber-Fechner law to plant processes. Again, no adequate picture is given of the physics of the material and energy exchange of the foliage leaf, a set of processes which BROWN and ESCOMB have, in the main, reduced to pure physics. In this connection, we find the author emphasizing BLACKMAN'S misleading statement that the foliage leaf under illumination maintains a temperature considerably above the surrounding air. This is possible if the evaporation power of the air or the water supply of the leaf is low. On the other hand, if the water supply of the leaf and the evaporation power of the air are high, the leaf will maintain a temperature below that of the surrounding air whether illuminated or not. In spite of the fact that the significant work of BROWN and ESCOMB has been much cited, it has failed to have a sufficient influence upon the statements in texts.

The book is marked by carefully guarded statements, which is certainly a virtue in any scientific work; but this is often carried to an exasperating extreme, involving guards where our knowledge is sure. It is seldom that a text is so free from personal hobbies of the author.

The greatest disappointment in the book lies in the apparently careless way in which it was finished. Minor errors are numerous. Careful reading of a very few pages shows a number of these: p. 203, the use of the old term "cyanophyll" for the term chlorophyllin; p. 204, "aqueous carbon dioxide" for aqueous solution of carbonic acid; p. 205, "fruit sugar" for grape sugar. In many cases a change in phrasing or in choice of words would make the description much more telling; p 204, the author speaks of the decomposition of CO_2 and H_2O when the thing to be emphasized is the *reduction* of carbonic acid. The need of the criticism of the manuscript by a number of physiologists is evident.—WILLIAM CROCKER.

NOTES FOR STUDENTS

Current taxonomic literature.—J. C. ARTHUR (Bull. Torr. Bot. Club **38**: 369–378. 1911) in continuation of monographic work on the North American rusts records new species in *Puccinia* and *Uromyces*. A "Key to American and European *Allium* rusts" is included in the article.—H. H. BARTLETT (Rhodora **13**: 163–165. 1911) has published a new species of *Euphorbia* (*E. arundelana*) from Maryland. The same author (*ibid.* 209–211. *pl. 93*) describes and illustrates a new species of *Oenothera* (*O. Tracyi*); the species is based on specimens grown from seed collected by S. M. TRACY near Tensaw, Ala.—W. H. BLANCHARD (*ibid.* 193–195) records a new variety of *Rubus* (*R. canadensis* var. *septemfoliolatus*) from Newfoundland; the same

author (*ibid.* 168–171) raises *Lycopodium complanatum* var. *flabelliforme* to specific rank, and (*ibid.* 55, 56) proposes a new name *Rubus amicalis* for *R. amabilis* Blanchard, not Focke.—T. S. BRANDEGEE (Univ. Calif. Pub. Botany 4:177–194. 1911) in continuation of his work on Mexican plants has published 42 new species of flowering plants and describes a new genus (*Lithophytum*), doubtfully referred to the Solanaceae.—J. BRIQUET (Ann. Conserv. & Jard. Bot. Genève 13–14:369–389 [29–49]. 1911) under the title "Decades plantarum novarum vel minus cognitarum" has published 11 new species of Caryophyllaceae and Labiatae from Mexico and South America.—N. L. BRITTON (Torreya 11:130, 152. 1911) records two new species of *Opuntia*, *O. jamaicensis* from Jamaica and *O. Tracyi* from Mississippi. The same author (*ibid.* 174) describes a new *Hernandia* (*H. catalpifolia* Britt. & Harris) from Jamaica.—F. BUBÁK (Ber. Deutsch. Bot. Gesells. 29:381–385. *pl. 14.* 1911) under the title "Ein neuer Pilz mit sympodialer Konidienbildung" describes and illustrates a new genus (*Acarosporium* Bubák & Vleugel) from Sweden. The fungus was found growing on dead leaves of *Betula odorata*.—R. E. BUCHANAN (Mycologia 3:170–174. *pls. 50, 51.* 1911) in an article on the "Morphology of the genus *Cephalosporium*" describes and illustrates a new species and variety of this genus; both were obtained by isolation from humus-rich soil and grown on dextrose agar.—B. F. BUSH (Rhodora 13:166–168. 1911) gives a synopsis of the Missouri species of *Rhexia*, recognizing three species, one (*R. latifolia*) being new to science.—J. CARDOT (Rev. Bryol. 38:49–52. 1911) under the title "Deux genres nouveaux de la région magellanique" describes two new genera of mosses, namely *Neuroloma* and *Hygrodicranum*.—C. CHRISTENSEN (Rep. Nov. Sp. 9:370–372. 1911) describes four new ferns, one (*Athyrium paucifrons*) being from Mexico.—F. S. COLLINS (Rhodora 13:184–187. 1911) under the title "Notes on algae" describes a new species in the genus *Dermocarpa* from Barbados, and one in *Chantransia* from North Carolina; and to the latter genus several species are transferred from *Acrochaetium*.—E. B. COPELAND (Phil. Journ. Sci. Bot. 6:65–92, 133–143, 145–148. *pls. 12–25.* 1911) has published some 65 new species of ferns from Borneo, the Philippine Islands, and Papua or New Guinea. Three new genera are proposed, namely: *Craspedodictyum*, *Dendroconche*, and *Merinthosorus*.—S. T. DUNN (Kew Bull. 310–313. 1911) describes a new genus (*Dipentodon*) from Yunnan, China; the genus is doubtfully placed in the Celastraceae.—W. W. EGGLESTON (Bull. Torr. Bot. Club 38:243, 244. 1911) describes two new species of *Crataegus* from Massachusetts.—A. W. EVANS (*ibid.* 205–222. *pls. 9, 10*) records 34 species of Hepaticae from the Bahama Islands, of which two are new to science; and (*ibid.* 251–286. *pls. 11, 12*) in an article entitled "Hepaticae of Puerto Rico" proposes two new genera, namely, *Leptocolea*, based on *Lejeunea micrandroecia* Spruce, and *Aphanolejeunea*, based on *Jungermannia microscopica* Tayl. Several new species and new combinations are included in the article.—M. L. FERNALD (Rhodora 13:109–162. *pls. 86–91.* 1911) gives a very interesting and significant account of a botanical expedition to Newfoundland and southern

Labrador during the summer of 1910. The author, after a careful study, concludes that "the indigenous flora of Newfoundland consists primarily of plants which occur to the north, in Labrador, or to the southwest, chiefly along the Atlantic seaboard or the Coastal Plain." Incidentally a new variety of *Carex* (*C. Hornschuchiana* Hoppe var. *laurentiana*) is recorded from Newfoundland and Anticosti.—M. L. FERNALD and K. M. WIEGAND (*ibid.* 188) record a new variety of *Epilobium* (*E. palustre* L. var. *longirameum*) from Labrador and Quebec.—F. W. FOXWORTHY (Phil. Journ. Sci. Bot. **6**:149–177. *pls. 26–33.* 1911) records 26 species of gymnosperms from the Philippine Islands, including a new species of *Podocarpus* and two hitherto unknown species of *Gnetum*.—T. C. FRYE (Proc. Wash. Acad. Sci. **12**:271–328. 1910) has published an illustrated taxonomic treatment of the "Polytrichaceae of western North America," recognizing for this region seven genera and about 26 species.—E. B. HARGER (Rhodora **13**:37–39. 1911) records a new species of *Arabis* (*A. viridis*) from New England.—H. HARMS (Rep. Nov. Sp. **9**:439, 440. 1911) has published a new species of *Poiretia* (*P. longipes*) from Brazil.—E. HEESE (Monats. für Kakteenk. **21**:132. 1911) describes and illustrates a new species of *Echinocactus* (*E. Gürkeanus*), introduced into European cultivation from Bolivia.—A. W. HILL (Kew Bull. 281–302. 1911) on "*Strychnos Ignatii* and other East Indian and Philippine species of *Strychnos*" recognizes about 24 species, some of which are new; a key to the species is included.—C. N. JENSEN and V. B. STEWART (Phytopathology **1**:120–125. 1911) in an article on "Anthracnose of *Schizanthus*" has published a new species of fungus (*Colletotrichum schizanthi*). The fungus was observed on various parts of *Schizanthus* at Ithaca, N.Y.—T. LOESENER (Rep. Nov. Sp. **9**:355–367. 1911) under the title "Mexikanische und zentralamerikanische Novitäten" has published several new species and varieties of flowering plants.—J. LUNELL (Am. Mid. Nat. **2**:122–128. 1911) records 4 new species and 8 new varieties of flowering plants from North Dakota and Minnesota.—A. H. MOORE (Bot. Jahrb. **45**:426, 427. 1911) gives a supplementary note on his recent monographic treatment of *Spilanthes*, recording further data on this genus, and includes descriptions of two new species from South America.—W. A. MURRILL (Mycologia **3**:165–169. *pl. 49.* 1911) under the heading "Illustrations of fungi IX" describes and illustrates several species, including a hitherto unrecorded species of *Hebeloma* (*H. praecox*) from New York; the same author (*ibid.* 189–199) in a third article on "The Agaricaceae of tropical North America" treats 6 genera, describing new species in *Clitocybe* (6), *Melanoleuca* (3), *Hydrocybe* (10), and *Hygrophorus* (2).—C. H. PECK (N.Y. State Mus. Bull. No. 150. pp. 100. *pls. 4, 6, 121–123.* 1911) presents the annual report of the state botanist for the year 1910, placing on record valuable data concerning particularly the flora of New York, and includes descriptions of 54 new species and varieties, mainly of fungi, but including also some flowering plants from different parts of the United States.—D. PRAIN (Kew [illegible] 317, 318. 1911) has published 2 new genera (*Cyrtogonone* an[illegible] of the

Euphorbiaceae from tropical Africa.—J. A. PURPUS (Monats. für Kakteenk. **21**:97–102. 1911) describes and illustrates a new species of *Mamillaria* (*M. valida*) from Mexico.—L. QUEHL (*ibid.* 119, 120. 1911) records a new species of *Echinocactus* (*E. nidulans*) from Mexico.—L. RADLKOFER (Phil. Journ. Sci. Bot. **6**:181–183. 1911) has published 4 new species of Sapindaceae from the Philippine Islands. The same author (Rep. Nov. Sp. **9**:372, 373. 1911) has described a new *Trichilia* (*T. stelligera*), and (*ibid.* 374–377) 5 new species in the Sapindaceae from Dutch Guiana.—C. B. ROBINSON (Phil. Journ. Sci. Bot. **6**:185–228. 1911) under the title "Botanical notes upon the Island of Polillo" gives a list of the plants known from this island and includes descriptions of 18 species new to science.—J. F. ROCK (Terr. Hawaii, Board Agr. & Forestry. Div. Forestry Bull. No. 1. pp. 1–14. *pls. 1–6.* 1911) records a new species of *Sapindus* and proposes a new genus (*Hibiscadelphus*) of the Malvaceae from the Hawaiian Islands.—R. A. ROLFE (Bot. Mag. t. 8392) has described and illustrated a new species of *Acineta* (*A. Moorei*) from South America.—E. ROSENSTOCK (Rep. Nov. Sp. **9**:342–344. 1911) has published 2 new species and a variety of ferns from Bolivia.—F. J. SEAVER (Mycologia **3**:207–230. *pls. 53, 54.* 1911) completes his consideration of "The Hypocreales of North America."—C. L. SHEAR (Phytopathology **1**:116–119. 1911) describes a new fungus (*Cryptosporella viticola*) which is said to be the cause of the so-called "dead-arm" of the grape.—P. A. SACCARDO (Ann. Mycol. **9**:249–257. 1911) under the title "Notae mycologicae" gives an annotated list of fungi, including descriptions of several new species, 4 of which are from New York and Florida.—V. SCHIFFNER (Oesterr. Bot. Zeitschr. **61**:261–264. 1911) in continuation of his studies on the genus *Metzgeria* records 2 new species from South America.—R. SCHLECHTER (Rep. Nov. Sp. **9**:428–439. 1911) has published several new species of orchids, including two from America and two from the Philippine Islands.—F. L. SCRIBNER (Bull. Torr. Bot. Club **38**:319–328. 1911) under the title "Notes on certain species of *Muhlenbergia*" records 2 new species in this genus from western United States and northern Mexico.—T. A. SPRAGUE (Bot. Mag. t. 8378. 1911) describes and illustrates a new species of *Columnea* (*C. gloriosa*) from Costa Rica. The plant has been introduced into cultivation at Erfurt, Germany, and at the Royal Botanic Gardens, Kew, England.—O. STAPF (Kew Bull. 318, 319. 1911) has published a new genus (*Sclerodactylon*) of the Gramineae from Madagascar.—F. STEPHANI (Hedwigia **51**:61–64. 1911) has proposed a new genus (*Goebeliella*) of Hepaticae, based on *Frullania cornigera* Mitt. The genus, as known at the present time, embraces two species, one from New Zealand, the other from New Caledonia.—G. SCWEINFURTH and R. MUSCHLER (Bot. Jarhb. **45**:428–430. 1911) propose a new genus (*Lifago*) of Compositae from Algiers.—H. and P. SYDOW (Ann. Mycol. **9**:142–146. *pl. 9.* 1911) under the title of "Novae fungorum species" have published several species new to science, including 4 from the Philippine Islands. The same authors (*ibid.* 277, 278) describe and figure a new generic type (*Scleropycnis*) which was found parasitic on branches

of *Abies excelsa* in the Erzgebirge.—I. URBAN (Bot. Jahrb. 45:432–470. 1911) in co-operation with several specialists, under the title "Plantae novae andinae imprimis Weberbauerianae V," has published 72 new species of flowering plants from South America.—WOOD and FRANKS (Kew Bull. 274, 275. 1911) have published a new genus (*Siphonochilus*) of the Scitamineae from Natal.—H. F. WERNHAM (Journ. Bot. 49:206–216. 1911) presents a revision of the American genus *Hamelia*, recognizing 27 species, of which one-third are characterized as new. The genus attains its greatest specific diversity in Mexico.—H. WOLFF (Rep. Nov. Sp. 9:417–422. 1911) under the title "Umbelliferae Novae I" has published several new species and proposes the following new genera from Mexico: *Nematosciadium*, *Schiedeophytum*, and *Langlassea*.—N. WORONICHIN (Ann. Mycol. 9:217–225. 1911) has characterized a new genus (*Physalosporina*) of the Pyrenomycetes. The genus, as at present understood, embraces 6 species having a distribution in the United States and Europe.—J. M. GREENMAN.

Biology of rusts.—The results of further studies on the biology of rusts are reported by FISCHER in two papers. The first one[6] is a continuation of a series of former studies, and includes four additional forms: *Uromyces caryophyllinus* (Schrank) Winter on *Saponaria ocymoides* L. and *Euphorbia Gerardiana* Jacq.; *Gymnosporangium tremelloides* Hartig on *Juniperus communis* L., *Sorbus Aria* (L.) Crantz, *S. chamaemespilus* (L.) Crantz, and the hybrid forms *S. hybrida* Koch (*S. aucuparia*×*S. Aria*) and *S. latifolia* (Lam.) Pers. (*S. Aria*×*S. torminalis*); *Ochrospora Sorbi* (Oud.) Diet. on *Aruncus sylvester* Kost. and *Anemone nemorosa* L.; and *Puccinia albulensis* P. Magn., a micro-*Puccinia* on *Veronica bellidioides* L. and *V. aphylla* L.

The discovery that the teleutospore generation belonging to *Aecidium Euphorbiae Gerardianae* occurs on members of the Caryophyllaceae serves as an illustration of the proposition formulated by FISCHER that on the hosts bearing the aecidial generation of certain heteroecious rusts there occur also micro- and lepto-forms whose teleutospores resemble the teleutospores of the heteroecious forms in question. The aecidium on *Euphorbia Gerardiana* has generally been regarded as belonging to *Uromyces excavatus* (DC.) P. Magnus on the same host; but the close resemblance between the teleutospores of *U. excavatus* and those of *U. caryophyllinus* occurring on members of the pink family led TRANZSCHEL to predict that the teleutospore form of *Aecidium Euphorbiae Gerardianae* would be found among the species of *Uromyces* parasitic on the Caryophyllaceae. The cultural work of FISCHER has shown the correctness of this prediction. It is probable that this resemblance, which has led to the discovery of the connection between aecidia and teleutospores in several cases, represents something more than a mere superficial similarity,

[6] FISCHER, ED., Beträge zur Entwicklungsgeschichte der Uredineen. Centralbl. Bakt. II. 28:139–152. 1910.

and may be an indication of phylogenetic relationship between such heteroecious forms and the corresponding micro- and lepto-rusts. The cultural work with *Aecidium Euphorbiae Gerardianae* further showed that there exists a certain degree of specialization among the forms of *Uromyces caryophyllinus*, for of several members of the pink family *Saponaria* was the only one that could be infected by aecidiospores from *Euphorbia Gerardiana*.

Gymnosporangium tremelloides had therefore been experimentally connected only with the aecidium on *Sorbus Aria*, although *Aecidium penicillatum* Müller occurs on a large number of pomaceous plants. The present work adds to *Sorbus Aria* three new aecidial hosts, two of which are probably hybrids, with *S. Aria* as one parent. *Ochrospora Sorbi*, which occurs on various species of *Sorbus*, has been connected with *Aecidium leucospermum* by TRANZSCHEL, but the form on *Aruncus* (*Spiraea*) *sylvester* had not previously been connected with that aecidium.

In the second paper[7] the author's studies on the biology of the forms of *Gymnosporangium* are continued. He finds that the *Roestelia cornuta* on *Sorbus torminalis* (L.) Crantz and *S. latifolia* (Lam.) Pers. has its teleutospores on *Juniperus communis* L. The small cushion-like sori occur on the leaves and resemble those of *Gymnosporangium juniperinum* L. The new form is distinct from both *G. juniperinum* and *G. Amelanchieris*, however, as neither of these produce aecidia on *Sorbus torminalis* and *S. latifolia*. The author proposes the name *G. tormanili-juniperinum* for it.

Cultures with *Gymnosporangium juniperinum* extend the list of aecidial hosts of this species to include *Sorbus americana* DC. and *S. hybrida* Koch, in addition to *S. aucuparia* L., which was previously known. On account of the successful infection of *Sorbus americana*, the author suggests that this form is identical with the form occuring on *Juniperus Sibirica* Burgsd. (*J. nana* Willd.) in America, as the American form was shown by ARTHUR to have aecidia of the *cornuta*-type on *Sorbus americana*. The American form is called by ARTHUR *S. cornutum* (Pers.) Arthur.

Further cultures with teleutospores of *Gymnosporangium Amelanchieris* show that this form does not infect *Aronia nigra* Kochne, and is therefore not identical with *G. Davisii* Kern, which has aecidia of the *cornuta*-type on *Aronia nigra*. In conclusion, the author points out the fact that often hybrids of an immune and a susceptible species are susceptible. This condition, however, is not universally true.

TRANZSCHEL[8] reports the following results of cultures made in the years 1906 and 1907. *Puccinia Porri* (Sw.) Winter, sown on its host *Allium Schoenoprasum* L., produced uredinia and telia directly, without first forming spermagonia or aecidia. This rust, therefore, is a true hemi-*Puccinia*, and the

[7] FISCHER, ED., Studien zur Biologie von *Gymnosporangium juniperinum*. Zeitschr. Bot. **2**: 753–764. 1910.

[8] TRANZSCHEL, W., Beiträge zur Biologie der Uredineen. III. Travaux Musée Bot. Acad. Imp. Sci. St. Pétersbour **7**: 1–10. 1910.

existence of true hemi-forms is thus definitely demonstrated. *Aecidium Liguloriae* Thüm. on *Ligularia Sibirica* Cass. was connected with *Puccinia Eriophori* Thüm. on *Eriophorum angustifolium* Roth. *Senecio paluster* DC. was also shown to be an aecidial host for this form. *Puccinia litoralis* Rostr. was shown to have aecidia on *Sonchus oleraceus* L., *S. asper* Vill., and *S. arvensis* L. *Puccinia Dietrichiana*, described as new, on *Agropyrum caninum* P.B., was connected with *Aecidium Trolli* Blytt on *Trollius europaeus* L. Two forms on species of *Carex* were connected with aecidia on species of *Centaurea*. These are *Puccinia Jacea-leporinae* on *Carex leporina* L. and *Centaurea Jacea* L.; and *Puccinia Jacea-capillaris* on *Carex capillaris* L., *Centaurea Jacea* L., and *C. nigra* L. A third form on *Carex gynobasis* Vill. was found among aecidia-bearing plants of *Centaurea orientalis* L. These and other known forms, whose alternate hosts are species of *Carex* and *Centaurea*, the author proposes to unite under the collective name *Puccinia Centaureae-Caricis*. The different forms are closely restricted to their respective host species. *Lepidium Draba* L. and *Cleome spinosa* Jacq. were added to the known aecidial hosts of *Puccinia Isiacae* (Thüm.) Winter. Successful sowings of that species were also made on *Nasturtium palustre*, *Thlaspi arvense*, *Stellaria media*, *Galeopsis Tetrahit*, and *Raphanus sativus* L. *Puccinia Caricis* (Schum.) Rebout on *Carex pallescens* L. produced aecidia on *Urtica dioica* L. The same species on *Carex vaginata* Tausch. produced aecidia on *Urtica dioica* L. and *U. magellanica* Juss. *Carex pallescens*, *C. vaginata*, and *Urtica magellanica* are new hosts for *Puccinia caricis*. *Puccinia Maydis* Bering produced aecidia on *Oxalis stricta* L. and *O. cormiculata* L. *Pucincia Poarum* Nielson on *Poa nemoralis* L. var. *firmula* Gaud. produced aecidia on *Tussilago Farfara* L., but not on *Petasites officinalis* Moench. The aecidium on *Petasites officinalis*, therefore, which has been associated by several authors with *Puccinia Poarum*, does not belong to that rust. New cultures with *Uromyces Rumicis* Winter on *Rumex obtusifolius* again showed that this rust has its aecidium on *Ficaria*, which is also the aecidial host for other species of *Uromyces*. A form of *Uromyces Dactylidis* Otth. was successfully sown on *Ranunculus repens* L. and *R. bulbosus* L., on both of which aecidia were produced. A number of cultures of *Puccinia Veratri* Duby, *P. glumarum* (Schmidt) Erikss. and Henn., *P. Iridis* (DC.) Wallr., and *P. oblongata* (Link) Winter gave negative results.

In Japan, ORISHIMO[9] has shown that *Peridermium Pini-densiflorae* P. Henn., common there on the leaves of *Pinus densiflora*, belongs to the species of *Coleosporium* on *Aster scaber* Thunb. Six other species of *Aster* on which species of *Coleosporium* occur were not infected by aecidiospores of this *Peridermium*. The form is separated as *Coleosporium Pini-Asteris*.

For students of the Uredinales, attention should be called to FISCHER's review[10] of work done on the biology of rusts in 1909.—H. HASSELBRING.

[9] ORISHIMO, Y., On the genetic connection between *Coleosporium* on *Aster scaber* and *Peridermium Pini-densiflorae* P. Henn. Bot. Mag. Tokyo **24**: 1–5. 1910.

[10] FISCHER, ED., Die Publication über die Biologie der Uredineen im Jahre 1909. Zeitschr. Bot. **2**:332–337. 1910.

Spore formation among the Fungi imperfecti.—LEININGER[11] studying the factors affecting the reproduction of *Pestalozzia Palmarum*, finds that this fungus has four modes of spore formation, whose manifestation depends upon the conditions under which the fungus is growing. Spore formation can always be induced by withdrawal of nutriment; the mode of spore formation, however, depends largely on the nature of the medium in which the fungus is growing or has been grown previous to spore formation. On submersed mycelia or on mycelia which are submersed after having grown on other media, true pycnidia are formed. Mycelia which have grown in liquid media also produce pycnidia when placed in a damp atmosphere. Mycelia growing in air on the surface of liquids, or on solid substrata, produce pseudopycnidia, i.e., fruiting organs with a pseudo-parenchymatous base, but whose upper part is composed of a thin layer of interwoven hyphae. Sori, which are never covered, and solitary spores are produced only on liquid media. Some organic substances seem to favor the production of one or the other of the last two modes of reproduction. The author suggests that the polymorphism of such forms necessitates a reform in the classification of the *Fungi imperfecti* on a physiological basis.

Another paper dealing with the instability of definite modes of reproduction among the *Fungi imperfecti* is that by VOGES,[12] who makes the difference in the spore-producing structures of two forms of *Hendersonia* a basis for a discussion of the validity of the characteristics used in the classification of this group. The two species discussed are *H. piricola*, a leaf-inhabiting form on the leaves of pear trees, and *H. sarmentorum*, which occurs on the dead stems of many plants. In *H. piricola* the spores are formed in the epidermal cells and become exposed by the breaking of the cuticle. They are borne in sori, therefore, with no vestige of a perithecium. In *H. sarmentorum*, however, a well-developed perithecium is formed. These two forms, although related in other characteristics, would thus fall into entirely different orders of the *Fungi imperfecti*, and therefore the author regards the presence or absence of the perithecium as a characteristic of subordinate importance. The form of the spores and the number of cells they contain he likewise regards as of minor importance.

Such variations are known to occur very frequently among the *Fungi imperfecti*, particularly in cultures of the more complex forms. As the classification of this group is one of convenience and does not involve a taxonomic problem in the phylogenetic sense, it would be an error to lay great stress on such deviations which occur under special conditions or in a few forms, and to subordinate to them such conspicuous characteristics as the presence of a perithecium, which on the whole serve well for the distinctions of large groups of forms as they occur in nature.—H. HASSELBRING.

---

[11] LEININGER, H., Zur Morphologie und Physiologie der Fortpflanzung von *Pestalozzia Palmarum* Cooke. Centralb. Bakt. II. 29:3–35. *figs. 15.* 1911.

[12] VOGES, E., Ueber die Pilzgattung *Hendersonia* Berk. Bot. Zeit. 68:87–100. *figs. 10.* 1910.

Symbiosis of ants and plants.—RIDLEY,[13] as director of the botanic gardens at Singapore, has had exceptionally good opportunities to examine the so-called "myrmecophilous plants" of the eastern tropics, and he has reported his studies of more than a dozen such cases of symbiosis. His observations appear to have been carefully made and accurately recorded, and must be regarded as a considerable contribution to our knowledge of the relationship existing between these two organisms, even if we do not agree with all his interpretations of the facts.

A very considerable number of such plants afford a convenient sheltering home for the ants, either within hollow organs, such as thorns or stems, or within the leaves or flowers. The ants, however, obtain no food from the plant, nor do they benefit it in any way. Examples of this class are *Dischidia Rafflesiana* and several species of rattan. In *Goniothalmus Ridleyi* it seems likely that the ants effect pollination while nesting in and about its flowers.

In the second class of myrmecophilous plants, there seems to be a relationship which is mutually advantageous between many epiphytic ferns and orchids, whose roots afford an excellent shelter, and the insects that, in constructing their nests, bring up considerable quantities of soil and heap it about the base of the plants. To this class belong *Thamnopteris nidus-avis*, *Platycerium biforme*, and a considerable number of orchids.

A third class consists of two small trees, *Macaranga triloba* and *M. Griffithiana*, whose hollow stems are pierced and tenanted by ants. In both species the stipules are persistent and possess glands which secrete waxy granules that the ants gather and use as food. In return for this shelter and food, RIDLEY declares that the ants protect the trees from the attacks of caterpillars, although his only evidence seems to be that the trees tenanted by ants were not damaged by caterpillars, while certain others had their leaves somewhat eaten. He concludes that "the hollow stem, the retention of the stipules for some time after their original function of protecting the bud has ceased to be necessary, and the production of food bodies, are all modifications which can have no other function than that of attracting the ants and retaining their services as guards."—GEO. D. FULLER.

Movement of water in plants.—In a brilliant and ingenious piece of work on the movement of water in plants, RENNER[14] has brought some telling evidence for DIXON's cohesion theory of the rise of sap. The evidence, too, is worked out by the use of that rather discredited instrument, the potometer. The cohesion theory, unlike the other conceptions of the rise of sap, has sound physics to recommend it, and now RENNER is able to measure suction in transpiring twigs amounting to 10–20 atmospheres, a thing that the cohesion theory assumes to exist. The "saturation deficit" is conceded by RENNER as the

---

[13] RIDLEY, H. M., Symbiosis of ants and plants. Ann. Botany **24**:457–483. 1910.

[14] RENNER, O., Experimentelle Beiträge zur Kenntnis der Wasserbewegung. Flora **103**:175–247. 1911.

cause of water movement. Whenever transpiration is occuring, a "saturation deficit" is produced in the cells of the region transpiring. This is the source of the "sucking power." When the loss of water is so great that the protoplast no longer exerts any pressure on the walls, the entire osmotic pressure of the cells is available for "sucking." The greatest suctions determined agree very closely with the osmotic pressures of the cells transpiring, as DIXON assumes to be the case. The method for getting the exact estimation of the greatest suction existing was ingenious. A twig that offered at one region great resistance to the movement of water (the resistance secured by tight clamping, double notching, or blocking of tracheae) was placed in a potometer. At a time when no "saturation deficit" existed, a determination was made of the rate of flow produced in the potometer by about 60 cm. of Hg. artificial suction. Through rapid transpiration the greatest "saturation deficit" was allowed to develop and the rate of flow it produced observed. The amount of suction involved in the second case could be figured from the known suction of the first, for it was found that the rate of flow was proportional to the suction. The maximum suction produced in forms like *Spirogyra* and *Helleborus* ranged from 10 to 20 atmospheres.—WILLIAM CROCKER.

Sand dunes of Illinois.—GLEASON'S[15] study of the vegetation of the sand deposits of Illinois is one of the most careful ecological surveys yet made of any region upon the continent. These deposits represent the most extensive areas with natural vegetation in the state, and cover over 8000 sq. km. The two most important types of vegetation are the grass lands, of which the bunch grass association, formerly covering nine-tenths of the entire sand area, is still conspicuous, and the forest, in which the black oak forms the typical association. This forest association, together with those composed of other species of oak which succeed it, are discussed elsewhere in some detail by HALL and INGALL[16], who give more emphasis to the economic than to the ecological aspect. It seems evident that the forest is slowly encroaching upon the prairie, although the advance of the oaks presents several unsolved problems. This tension line between forest and prairie is but one expression of the diverse elements of vegetation here in close contact, showing the unique position occupied by Illinois as a meeting ground for the great vegetational provinces of the north, south, east, and west.

Not only have the larger relationships existing between formations and associations received attention, but a careful analysis of the composition of each association is made, and the importance of the various constituent species estimated by the detailed study of many quadrants. An extensive list of these species is well annotated.—GEO. D. FULLER.

---

[15] GLEASON, H. A., The vegetation of the inland sand deposits of Illinois. Bull. Ill. State Lab. Nat. Hist. 9:23–174. *pls. 1–20. figs. 6.* 1910.

[16] HALL, R. CLIFFORD, and INGALL, O. D., Forest conditions in Illinois. Bull. Ill. State Lab. Nat. Hist. 9:175–253. 1911.

Ecology of Australian algae.—The Yan Yean Reservoir, with an area of 1460 acres and an average depth of 24 feet, furnishes part of the water supply for the city of Melbourne, distant about 25 miles. From regular collections made from its waters for a period of 13 months, WEST[17] has studied the composition, distribution, and periodicity of its phytoplankton and its littoral algal flora. The most striking feature of the plankton is the richness of its desmid flora. The desmids reach their dominance during the warm period, from February to May, and their minimum during the succeeding cold months from June to October. During this cold period the crustaceans are dominant. The absence of the usual blue-green algal element at all times of the year is another noteworthy feature of the plankton.

The littoral algal flora is rich in species, contains many interesting types, and exhibits three rather well marked phases during the year. From November to January, with a rising temperature, there is a dominance of the Oedogoniaceae and Zygnemaceae, with an increasing quantity of the Desmidiaceae; these last reach their climax during the following warm months. The cold months of September and October show very little algal life. Of the 300 or more species of algae collected, 14 species and 11 varieties are described for the first time.—GEO. D. FULLER.

Vegetation of the Kermadec Islands.—From their position midway between New Zealand and the Polynesian Islands, these small islands of volcanic origin and subtropical climate exhibit many features of botanical interest. Sunday Island, the largest of the group, with an area of about 30 sq. km., has been visited by OLIVER,[18] who spent ten months studying the vegetation. An annual rainfall of about 225 cm., well distributed throughout the year, with the mild climate, produces a forest composed entirely of broad-leaved evergreens, with a conspicuous number of epiphytes. Among the tree members of this formation, two endemic tree ferns (*Cyathea*) are conspicuous, attaining a height of 20 m., and appearing as the dominant members of one of the forest associations. The epiphytes are principally filmy and other ferns. Only 12 of the 114 species of vascular plants are endemic, a small proportion when compared with the flora of other isolated Pacific islands, and this fact, along with certain geologic evidence, leads to the conclusion that the islands are not older than the Pliocene. The relationship of their flora with those of New Zealand, Australia, and Polynesia is traced.—GEO. D. FULLER.

Vegetation in the Dovrefjeld.—During a month spent in the upper Driva Valley, the WESTS[19] made an ecological survey of the alpine associations of

[17] WEST, G. S., The algae of the Yan Yean Reservoir, Victoria; a biological and ecological study. Jour. Linn. Soc. **39**: 1–88. *pls. 6. figs. 10.* 1909.

[18] OLIVER, REGINALD B., Vegetation of the Kermadec Islands. Trans. New Zealand Inst. **42**: 118–175. *pls. 18–33.* 1909.

[19] WEST, W. and G. S., Sketches of vegetation at home and abroad V. The ecology of the upper Driva Valley in the Dovrefjeld. New Phytol. **9**: 353–374. *pls. 3, 4. figs. 23–32.* 1910.

the mountain slopes rising from partially cultivated rocky pastures near the river. A belt of woodland occupies the valley slopes up to an altitude of about 3600 feet, the montane forest consisting of *Betula odorata*, reaching a maximum height of 20 feet, with an undergrowth of *Betula nana*, *Juniperus nana*, *Empetrum nigrum*, and various species of *Salix* and *Vaccinium*, together with a rather abundant herbaceous vegetation. The shrubby members of this association persist in the belt of alpine shrubland, which reaches a poorly defined upper limit (4500–4800 ft.) with the disappearance of its most persistent members, *Salix reticulata* and *Betula nana*. Above is a luxuriant alpine lichen association, affording pasture for the reindeer and dotted with a variety of alpine flowers. Among the notes upon the many species examined, the scarcity of *Sphagnum* even in bogs is emphasized, and the results of a study of the variation at different altitudes of the leaves of *Betula nana*, both in size and structure, are recorded.—GEO. D. FULLER.

Parthenogenesis in Bennettites.—In 1894 LIGNIER published an account of the structure and affinities of *Bennettites Morieri*, and now, upon looking over his former preparations, he has come to the conclusion that the species was parthenogenetic.[20] The evidence is that the nucellar beak is not perforated or disorganized in any way, but is an absolutely continuous mass of primary tissue, that is, not tissue arising by proliferation and filling a passageway. The pollen chamber forms within the beak and extends more or less toward its tip, but never reaches the surface, so far as the author's preparations show. This is taken to prove that the observed embryos have developed in the absence of pollen tubes; it is recognized that they may or may not be parthenogenetic in the sense of arising from an unfertilized egg. It is further suggested that the parthenogenetic habit may have been the chief cause of the rapid disappearance of a group that was so flourishing during the Jurassic.—J. M. C.

Permeability.—CZAPEK[21] has brought together all his work on the effect of the surface tension of the surrounding fluid on the permeability of the Plasmahaut of the plant cell. Reviews[22] of preliminary articles have given the main points of this paper. Some evidence is offered that acids have their effect by interfering with the Plasmahaut emulsion. CZAPEK also doubts TRAUBE'S conception of osmosis, though his experiments offer little evidence against it. Many more substances were found which produced exosmosis of the cell contents of phanerogams only when their aqueous solutions had a surface tension of 0.68 (or less) of that of water. The Plasmahaut of

[20] LIGNIER, O., Le *Bennettites Morieri* (Sap. et Mar.) Lignier se reproduisait probablement par parthénogénèse. Bull. Soc. Bot. France **58**:224–227. 1911.

[21] CZAPEK, F., Ueber eine Methode zur Bestimmung der Oberflächenspannung der Plasmahaut von Pflanzenzellen. 8vo. pp. iv+86. *figs. 3.* Jena: Gustav Fischer. 1911. M. 2.60.

[22] BOT. GAZ. **50**:234. 1910, and **51**:472. 1911.

yeast apparently has a surface tension of about 0.60. The article seems to clear away much of the haze that has surrounded the matter of the significance of surface tension in cell activity.—WILLIAM CROCKER.

Underground organs of weeds.—Conflicting statements by various authors have induced PAMMEL and FOGEL[23] to investigate the organs of vegetative reproduction of some of our most common weeds. The Canada thistle (*Cirsium arvense*), the horse nettle (*Solanum carolinense*), the milkweed (*Asclepias syriaca*), and the bindweed (*Convolvulus arvensis*), were all found to be propagated by horizontal roots bearing adventitious buds; while in the wild morning glory (*Convolvulus Sepium*) and the quack grass (*Agropyron repens*), the organs of vegetative multiplication are rootstocks. In some instances the roots and subterranean stems resembled each other so closely that only by microscopic examination could the difference be detected.—GEO. D. FULLER.

Epidermis and light refraction.—FRIMMEL[24] thinks he has shown that the lower papillate epidermis of the leaves of the yew gives a total refraction of the light passing through the leaf from above, thereby leading to the use of all light that enters the leaf. He relates this character to the ability of the tree to grow in shaded habitats. He believes the lower epidermis of a number of other conifers acts in the same way. He finds a similar contrivance in the spongy parenchyma of the cotyledon of the beech. The fact of total refraction in the yew seems entirely established; whether it is of biological significance or not is quite another question.—WILLIAM CROCKER.

Arctic vegetation.—Hare Island off the coast of West Greenland, an uninhabited island 66 square miles in area, has been visited several times by PORSILD,[25] who has found a flora consisting of 82 arctic and 30 subarctic species. The vegetation belongs to the fell-field formation, large areas quite devoid of plants, passing into a poorly developed heath with arctic meadows and bogs in the more sheltered situations. Dispersal is almost entirely through the agency of the wind over the surface of the snow and frozen seas. The subarctic species are regarded as relics of milder climate in post-glacial times.—GEO. D. FULLER.

Pneumatophores.—From an examination of the tissues of vertical apogeotropic branches of the roots of *Terminalia Arjuna*, a large tree of Central India,

---

[23] PAMMEL, L. H., and FOGEL, ESTELLE D., The underground organs of a few weeds. Proc. Iowa Acad. Sci. **16**: pp. 7. *pls. 5.* 1909.

[24] FRIMMEL, FRANZ V., Die untere Kutikula des *Taxus*-Blattes ein Lichtreflektor. Oester. Bot. Zeitsch. **61**: 216–223. *figs. 4.* 1911.

[25] PORSILD, MORTEM P., The plant life of Hare Island off the coast of West Greenland. Saertryk af Meddelelser om Gronland **47**: 252–274. *figs. 10.* Kobenhavn: Bianco Lunos. 1910.

ADAMSON[26] decides that they are developed "for purposes of aeration as shown by the great development of lacunar tissue." Both the horizontal and the vertical roots possess very loose cortical tissue with large lacunae, but most botanists would probably hesitate to pronounce upon the purpose of its development. The upright roots have well developed root caps, and possess no lenticels or other stem characters found in many pneumatophores.—GEO. D. FULLER.

Seed of Neuropteris.—In 1904 KIDSTON described the seed of *Neuropteris heterophylla*, which was said to be "as large as a hazelnut." Now the same investigator, associated with JONGMANS, has described[27] the seed of *N. obliqua* Brong., the specimens being in the Rijks Herbarium at Leyden. The seeds have the same general structure as those of *N. heterophylla*, but are about twice as large. This species of *Neuropteris* is also doubtless to be referred to the stem genus *Medullosa*.—J. M. C.

Root parasites.—MISS BENSON[28] has studied the structure of some haustoria on the roots of *Exocarpus* and *Thesium*, showing the nature of the penetration and connection with the roots of other plants. For a portion of the lignified elements of the haustoria the name "phloeotracheids" is suggested, and the investigator thinks they may act as a filter between the host and parasite, although the evidence that they have any such function does not seem to be at all convincing.—GEO. D. FULLER.

Calcium salts and fungi.—WEIR[29] concludes that soluble calcium salts are necessary to the complete development of higher fungi. *Coprinus plicatilis*, *C. papillatus*, *C. nivens*, and *C. ephemoides* showed little if any mycelial development, and no development of fruit heads or spores, when all the calcium present was in the form of the oxalate.—WILLIAM CROCKER.

A bog in central Illinois.—GATES[30] has instanced the meeting of northern and southern forms in a bog in central Illinois.—GEO. D. FULLER.

---

[26] ADAMSON, R. S., Note on the roots of *Terminalia Arjuna*. New Phytol. **9**: 150–156. *figs. 3–7*. 1910.

[27] KIDSTON, R., and JONGMANS, W. J., Sur la fructification de *Neuropteris obliqua* Bgt. Archiv. Néerl. Sci. III. B. **1**: 25, 26. *pl. 1*. 1911.

[28] BENSON, MARGARET, Root parasitism in *Exocarpus* (with comparative notes on the haustoria of *Thesium*). Ann. Botany **24**: 667–677. *pl. 65. figs. 4*. 1910.

[29] WEIR, JAMES R., Benötigt der Pilz *Coprinus* Kalksalze zu seinen physiologischen Funktionen. Flora **103**: 87–90. 1911.

[30] GATES, F. C., A bog in central Illinois. Torreya **11**: 205–211. 1911.

VOLUME LIII NUMBER 2

THE

BOTANICAL GAZETTE

FEBRUARY 1912

THE LIBERATION OF HEAT IN RESPIRATION

GEORGE J. PEIRCE

(WITH EIGHT FIGURES)

In September 1908, the BOTANICAL GAZETTE[1] published an account of some preliminary experiments, of a qualitative sort, in which I had used silvered Dewar flasks as respiration calorimeters. Continued experimenting with these flasks, and the reports of correspondents, have further confirmed their usefulness in physiological laboratories. They have also led me to doubt whether, after all, a study of the heat yield alone will lead one very far toward a solution of the problems presented by respiration.[2] In this paper, however, I propose to give the data of some of my experiments, continuing and extending the work previously reported, and after that to discuss the possible significance of the results.

The quantity of heat liberated by germinating peas

In the preliminary paper already referred to, my experiments were necessarily rough, in accuracy below the efficiency of the apparatus, which, however, was used under laboratory conditions and not under constant temperature. The necessity of working in a constant temperature is apparent, when any attempts to determine heat yields is being made, since the experiments continue through several days. Constant temperature rooms are generally hard to secure and hard to keep clear of fungus spores, bacteria, etc.

[1] BOT. GAZ. 46:205–220. 1908.

[2] Plant World 12:193–198. 1909.

The Botanical Department of this University has been particularly fortunate in falling heir to two large chambers, the temperature of which has been remarkably constant during the months in which temperature records have been kept. These rooms are underground, built of concrete, and were used at one time as tanks in which fuel oil was stored. With a change in the means of heating our building, these tanks ceased to be used. The site of the experiment house, which was built in the summer of 1908, was so selected that these two tanks came under the floor of the greenhouse. The tanks were then cleaned of the residual fuel oil, and were ready for use as constant temperature chambers when the house over them was completed. Each is entered through a manhole in the floor of the greenhouse, the descent being over an iron ladder. Walls, floor, roof, and ladder are of such material that they may be washed or hosed off with an antiseptic solution, which may then be quickly swabbed up. The air, never excessively dry, can easily be maintained at any degree of humidity that one chooses, by occasionally sprinkling the walls. The following table will indicate the temperatures in one of these tanks during a period of nearly five months, these temperatures being taken by a maximum-minimum thermometer of the United States Weather Bureau pattern.[3] They are as follows:

Date	Time	Room	Maximum	Minimum	Differences
March 26....	....	16.4°C.	......	......	......
March 28....	10:00 A.M.	16.25	17.22°	16.67°	0.55°
March 29....	9:30 A.M.	16.2	17.11	16.61	0.50
March 30....	....	16.2	17.11	16.61	0.50
March 31....	....	.....	17.05	16.55	0.50
April 1.....	....	.....	17.22	16.55	0.67
April 2.....	....	.....	17.22	16.50	0.72
May 12......	....	......	18.89	17.78	1.11
May 13......	....	.....	18.89	18.05	0.34
May 14......	....	.....	18.61	18.05	0.56
May 15......	....	.....	18.61	18.05	0.56
May 16......	....	.....	18.83	18.05	0.78
May 17......	....	.....	18.77	17.73	0.94
May 18......	....	.....	19.07	17.91	1.06
August 13....	10:30 A.M.	20.5	20.55	17.78	....

Inspection of this table shows that the lowest maximum was on March 31, a temperature of 17.05° C. The lowest minimum was

[3] Bausch & Lomb Optical Co.'s Catalogue, no. 17,004.

two days later, April 2, a temperature of 16.50° C. The highest maximum came at some time during my absence in the summer vacation, a temperature of 20.55° C., which, however, differed from the temperature at the time I made and recorded the observation on August 13 by only 0.05°. The highest minimum was in mid May. Between the highest and lowest maxima there was a difference of 3.5°; between the highest and lowest minima a difference of 1.55°; and between highest maximum and lowest minimum a difference of 4.05° from late March to mid August, with an average daily range of 0.71° on 13 days in March, April, and May. It is needless to say that these chambers might be warmed, and presumably their temperatures would be very nearly as constant, but in this mild climate, in which there is little frost even at night in midwinter, and still less excessive heat in midsummer, artificial heat seems unnecessary, at least for experiments on the respiration of such germinating seeds as peas.

Having thus established the remarkable constancy in the temperature of these chambers, I may now pass to a consideration of the apparatus employed. I have used silvered Dewar flasks made by Burger of Berlin and imported "duty free." These Burger-Dewar flasks are stamped and numbered by the maker. Their efficiency is very uniform. Experience with the unsigned flasks of other makers quickly shows that they are not so uniformly efficient as they should be. For the sake of convenience and economy, not at first realizing my mistake, I have continued to use flasks of about 250 cc. capacity. But I am sure that flasks of not less than double this capacity would be more satisfactory because involving smaller physical errors.[4] Most of the flasks are simply double-walled round-bottom flasks, like fig. 1, but I have had four made in which, as indicated by fig. 2, the interior drains through a tube opening at *a*. This opening is small, but it seems to be sufficient to carry off carbon dioxide as well as water. At the same time, it does not greatly reduce the efficiency as an insulator of a well-made flask, and does add materially to its convenient use, making it possible to

[4] See OSTWALD-LUTHER, Physikalisch-chemische Messungen 2:189, 1902, where BERTHELOT's results are cited as indicating that it is not practicable to use calorimeters of less than half-liter capacity.

soak seeds in the flask, and then, when one is ready, to draw off the water without exposing or disturbing the other contents. The efficiency of silvered double-walled Dewar flasks used as insulators is indicated by the following experiment. Four flasks, numbered 1, 3, 4, and 6, held in pairs in the wooden filter stands usual in chemical laboratories, were set on a table in my laboratory. Into each were introduced 140 cc. of hot, distilled water; a long thermometer reading to tenths of a degree was placed in each flask and held, with the bulb almost touching the bottom, by a tight plug of absorbent cotton placed in the neck. The successive thermometer readings and other data follow:

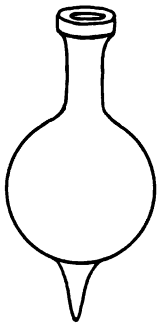


FIG. 1

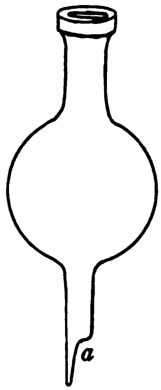


FIG. 2

Flask	August 26, 1909				August 27, 1909	September 1, 1909
	11:30 A.M.	1:45 P.M.	3:05	5:05	11:05 A.M.	2:15 P.M.
1.........	72.4°C.	67.05°	64.4°	60.8°	41.0°	21.4°
3.........	73.1	61.75	56.7	50.6	27.4	21.0
4.........	60.05	54.0	51.12	47.5	Hg col. separated	.....
6.........	63.4	57.6	54.74	51.0	20.5	20.75
Room.....	21.11	20.75	21.2	20.75	20.5	20.75

A similar experiment is recorded in the following table, in which drained flasks were used in constant temperature room A:

Flask	April 18, 1910		April 19, 1910	
	11:04 A.M.	12:05 P.M.	12:20 P.M.	4:15
11–5....................	68.7°	65.6°	32.4°	30.2°
12–2....................	72.7	69.9	38.6	36.25
14–6....................	61.1 (broke)	46.9	17.8	17.8
8–8....................	51.15	49.9	30.7	28.9
Room....................	17.0	17.5	17.3	17.3

The graphic representation of these figures, as in the accompanying curves (figs. 3 and 4), indicates more plainly the different degrees of efficiency as insulators possessed by different flasks, even of the same manufacture. The record of flask 14 with thermometer 6, in fig. 4, shows very strikingly the part played by the vacuum as an insulator between the two silvered walls of these

Fig. 3.—Graphic representations of temperatures in silvered Dewar flasks and in the laboratory.

double-walled flasks, for I cracked this just after pouring in the warm water. Although I kept the water in the inner flask, the vacuum surrounding it was destroyed. The temperature fell to approximately that of the room, almost as rapidly as in a single-walled unsilvered vessel. For obvious reasons, the rate of fall in temperature is most rapid when there is the greatest difference in the temperatures within and without the flask. This fact is impor-

FIG. 4.—Graphic representations of temperatures in silvered Dewar flasks and in the constant temperature room

tant in connection with respiration experiments in which heat production is being studied; for evidently the flasks, as well as the organisms within them, will lose heat most rapidly through the air when the air is decidedly cooler than they are, whether because the air is actually cold, or because the heat liberated by the organisms in the flask accumulates. The total heat liberated, therefore, must be the sum of the heat lost through radiation, etc., plus that retained by the flask. By placing the flasks in a constant temperature, the rate, and therefore the amount, of heat-loss can be determined for each flask and each degree of difference in temperature.

Another factor to be reckoned before we can attempt even approximately to determine heat yields is the heat equivalent of each combination of apparatus. This work has revealed to me, as I never suspected before, the limitations of the ordinary thermometer as an instrument of precision. In the following determinations, as will be seen below, I have used the same thermometers and the same cotton plugs in the same flasks throughout the series of experiments, thus determining the heat equivalents of each calorimeter, consisting of thermometer, Dewar flask, and plug. Indeed, I kept the flasks in the same places on the wooden filter stands and even on the same spot on my table. These latter precautions are, however, strainings at gnats, for the camel of unavoidable error to be swallowed is very large, owing to the small size of the flasks.

The method followed to ascertain the heat equivalent of each set of apparatus was fundamentally as follows, although I modified one detail or another in the series of determinations which I attempted. Into a flask, the temperature within which is known and recorded, 200 cc. (100 cc. if the flask already contains 100 cc.) of warm distilled water, at a known temperature, are *quickly* poured; the temperature within the flask is again recorded, as soon as it has again become fairly stable. The fall in the temperature of the water poured into the flask indicates that the flask and the inclosed air, thermometer, and cotton plug, have taken up warmth from the water. If all the water could be delivered into the flask at the temperature recorded, the fall in temperature would indicate only the amount of heat taken from the water by the apparatus. But this ideal condition I have found practically unattainable.

Working with only 200 cc. of water, at the most, I have never been able to pour this water from the flask in which it was heated into the Dewar flask so quickly that no heat was lost. I used a thin-walled round flask for heating the measured quantity of water; I cut the neck of the flask to a length of 2 cm.; while being heated the flask was held by a small wooden test tube holder of the usual form; the thermometer for determining the temperature of the water remained with its bulb under water in the flask while it was heated; and I took pains not to let the flask touch anything after taking it from the flame, until it was emptied. By holding the flask with the wooden holder while the water in it was warming, I warmed the holder, and as wood is a non-conductor, I felt that I was taking the least possible heat from the water myself in pouring it. In these and in other ways, therefore, I have taken such pains as I could to reduce the inevitable error to its lowest terms; but the error in calorimetry is stated by LUTHER-OSTWALD to be about 1 per cent under the most favorable conditions, and with larger volumes of liquid than I have so far been able to use. A typical series of figures follows, with the averages of a considerable number of determinations for four calorimeters.

April 2, 1910	No. 11–5	No. 12–2	No. 14–6	No. 8–8
Temperature, empty	27.6°	29.2°	29.1°	28.7°
Add 200 cc.	45.0	42.0*	42.0	40.
Becomes	43.2	40.75	40.5	38.55
Loss	1.8	1.25	1.5	1.45
Calories lost	360.0	247.0	300.0	290.0
Gain temperature	15.6	11.55	11.4	9.85
Calories per degree	23.07	21.4	26.3	29.4

* Measured 197 cc.

The averages for four calorimeters follow:

No. 11–5, 15 determinations average 24.7 calories per °C.
No. 12–2, 15 " " 24.4 " " "
No. 14–6, 10 " " 24.8 " " "
No. 8–8, 13 " " 28.5 " " "

The average of these four calorimeters is 25.6 calories per Centigrade degree. This means that the average calorimeter, consisting of a silvered Dewar flask of 250 cc. capacity made by Burger of Berlin, a long thermometer graduated to tenths of a degree, and a cotton plug suitable to close the neck of the flask, required a quan-

tity of heat represented by about 25 calories to warm its interior 1° C. Thus, if the temperature in one of these calorimeters goes up 10° C., about 250 calories had been taken by the apparatus itself. This is known as the "heat equivalent" of the apparatus, and is a quantity which must always be added or subtracted in determining the amounts of heat liberated or taken up by a given organism, process, or reaction.

In addition to the heat lost by radiation, etc., from the insulating calorimeter, and the heat absorbed by the whole apparatus (flask, thermometer, and plug) and the air contained by it, the material within the flask will also absorb heat. It is necessary, therefore, to determine the heat equivalents of the material worked with, whether these materials are seeds or solutions. The solutions may contain nutritious substances in which such organisms as bacteria, yeasts, or fungi are living. In any case, the heat equivalents of all the substances or materials involved in the experiment must be ascertained. Thus, on one day I weighed out six lots of air-dry peas of 75 gr. each, putting these in crystallizing dishes, which I covered with glass lids and kept for 24 hours at a temperature of about 18° C. Six Dewar flasks with thermometers and plugs, and containing some distilled water, were also placed under the same condition. After 24 hours I drained (but did not dry) the flasks, and put one lot of peas in each, reading the temperature of each. I assumed that the peas had in this time taken on a uniform temperature before being put into the flasks. The slight differences in temperature, therefore, were presumably due to slight differences in the temperatures of the flasks and to slight differences in the amounts of heat due to friction in pouring the air-dry peas into the flasks. Then I poured 100 cc. of warm distilled water at a known temperature into each flask and, when the temperature had become stable, recorded it. The data are as follow:

Flask	Therm.	Temp.	100 cc. aq.	Becomes	Loss
1...........	1	19.7°	57.0°	45.3°	1170 cals.
2...........	2	19.2	55.5	43.5	1200
3...........	3	19.3	56.0	44.2	1180
4...........	4	19.5	54.0	43.0	1100
5...........	5	19.8	52.0	41.2	1080
6...........	6	19.8	49.5	40.4	910

From these figures and from the previous determinations of the average number of calories required to raise each set of apparatus one degree in temperature, I calculated the number of calories required to raise 75 gr. of air-dry peas 1°. These figures and the average follow:

To raise 1° requires:

1 = 45.70	calories less average no. calories required to raise	1 − 1° − 11.62 = 34.08c
2 = 49.38	" " " " " " " "	2 − 1° − 13.25 = 36.13c
3 = 47.78	" " " " " " " "	3 − 1° − 12.81 = 34.97c
4 = 46.80	" " " " " " " "	4 − 1° − 13.49 = 33.31c
5 = 50.46	" " " " " " " "	5 − 1° − 11.67 = 38.79c
6 = 44.17	" " " " " " " "	6 − 1° − 10.54 = 33.73c
Total	. . . .	211.01c
Average to raise 75 gr. air-dry peas 1°	. . . .	35.16c
" " " 1 gr. " " 1°	. . . .	0.4688c

From this it appears that it takes 0.468 of a calory to raise one gram of air-dry peas 1° in temperature. A repetition of the experiment with the same apparatus and under similar conditions gave an average of 0.457 of a calory per gram of air-dry peas.

The same experiment was repeated on a later date with this modification; 6 lots of air-dry peas weighing 75 gr. each were put in the same 6 Dewar flasks and washed in a concentrated aqueous solution of mercuric bichloride. After rinsing twice with boiled distilled water, the peas were covered with 100 cc. of boiled distilled water in each flask, thermometers and cotton plugs were inserted as usual, and the whole allowed to stand for 24 hours in the laboratory. The temperatures in the flasks and in the room at the hours stated were as follow:

Flask	March 10, 1909			
	12:00 M.		2:00 P.M.	
1	16.0°	Room 18°	16.55°	Room 20.5°
2	16.0	....	16.50	....
3	16.0	....	16.70	....
4	16.8	....	17.20	....
5	17.5	....	18.10	....
6	17.5	....	18.05	....

The next day the temperatures were recorded as below, and 100 cc. of warm distilled water at the temperatures reported were poured into each flask. Flask 5 exploded at this stage. The following figures indicate the heat equivalents of the five remaining lots of peas, and these yield an average of 1.41 calory per degree for 75 gr. of peas weighed air-dry and soaked for 24 hours in 100 cc. of boiled distilled water. This figure would be the sum of the heat equivalent of pea substance weighed air-dry and water, if no change had taken place in the substance of the peas during this interval of 24 hours in water; but assuming, for the moment at least, the correctness of the figure 1.41 calory per degree, one must realize that in this time germination had begun, and that the materials in the peas had begun to undergo changes, not only from absorption and the solution or dilution of the soluble substances in the peas, but from digestion and other metabolic processes. The figure 1.41 calory per degree, therefore, may be correct or approximately so, for peas which had been for 24 hours under conditions favorable to germination, and hence were not necessarily identical in composition with air-dry peas of the same variety.

March 11, 1909, 9:30 A.M.; room 15.75°

1........	18.7°	100 cc. aq. 64.3°	Becomes 39.12°	Loss 2518 cal.
2........	18.4	56.4	35.9	2050
3........	18.4	60.2	37.8	2240
4........	19.4	58.5	37.6	2090
5........	19.3	Exploded		
6........	19.4	56.0	35.7	2030

To raise 75 gr. peas soaked 24 hrs. *in situ* 1° requires:

1—123.11	calories less average for flask 1 and therm. 1—11.62	= 101.49 cal.
2—116.42—13.25	" " " " " 2 " " 2	= 103.17 "
3—114.87—12.81	" " " " " 3 " " 3	= 102.06 "
4—114.83—13.49	" " " " " 4 " " 4	= 101.34 "
6—123.78—10.54	" " " " " 6 " " 6	= 113.24 "
Average for 75 gr. peas soaked per degree	. . . . . .	= 106.26 "
" " 1 " " " " "	. . . .	= 1.41 "

I think we are now ready to proceed to ascertain the heats liberated by peas from the beginning of germination until it has progressed for several days. An experiment was set up as follows:

March 26, 11:30 A.M.; room temperature 16.4° C. Five lots, 75 gr. each, of air-dry peas were kept in constant temperature room A for a week, in five Dewar flasks. Thermometers, bottles of boiled distilled water, and of saturated aqueous solutions of mercuric bichloride, had been placed in room A at the same time, and were therefore of like temperature. Each lot of peas was then thoroughly washed in the bichloride solution, rinsed twice with boiled distilled water, and covered with 100 cc. of boiled distilled water in each flask. (The rinsing water came from the laboratory and had a temperature 2° C. higher than that put in the flasks to start germination.)

The temperatures were:

Flask 1, therm. 1, 17.4°
" 2 " 2, 17.3
" 3 " 3, 16.9
" 4 " 4, 18.4
" 6 " 6, 17.5

MARCH 27, 10 A.M.; ROOM 16.25°

1	18.9°	−37.0 cc.	Absorbed 63.0 cc. aq.
2	18.7	−44.0	" 56.0
3	17.55	−40.5	" 59.5
4	18.3	−45.4	" 54.6
6	18.4	−45.5	" 54.5

I poured off the unabsorbed water in each flask as indicated above, showing that each lot of 75 gr. of air-dry peas had absorbed the number of cc. of water above stated. The rise in temperature in each flask showed the liberation of heat. Reckoning the heat equivalents already found of the pieces of apparatus, the peas, and the water, we find that there were liberated in each flask the following quantities of heat, plus whatever had been lost by radiation through the flasks, by leakage through the cotton plugs, etc., in the first 22.5 hours of the experiment, namely:

1	1.5°	218.55 calories
2	1.4	96.00
4	0.00	0.00
6	0.9	129.75
Average		130.68 calories

MARCH 28, 10 A.M.; ROOM 16.25°

	No.	Temp.	Gain in 24 hrs.	Total gain
1	23.8°	4.9°	6.4°	......
2	24.7	6.0	7.4	......
3	20.4	2.85	3.5	......
4	21.2	2.9	2.9	......
6	22.1	3.7	4.6	......
Average		4.07	4.96	482.71

MARCH 29, 9:30 A.M.; ROOM 16.2°

1	32.3°	8.5°	14.9°	......
2	38.55	13.85	21.25	......
3	25.00	4.6	8.1	......
4	25.9	4.7	7.6	......
6	29.4	7.3	11.9	......
Average		7.79	12.95	923.90

MARCH 30, 9:00 A.M.; ROOM 16.2°

1	39.0°	6.7°	21.6°	......
2	45.1	6.55	27.80	......
3	30.25	5.25	13.35	......
4	31.8	5.9	13.5	......
6	36.7	7.3	19.2	......
Average		6.34	19.09	751.95

MARCH 31, 1909, 9:30 A.M.; ROOM 16.1°

1	40.9°	1.9°	23.5°	
2	50.8	5.7	33.5	
3	32.6	2.35	16.7	
4	32.3	0.50	14.0	
6	37.25	0.55	19.75	
Average		2.20	21.49	[illegible]

APRIL 1, 1909, 9:30 A.M.; ROOM 16.4°

1	41.3°	0.4°	23.9°	
2	52.55	1.75	33.25	
3	33.1	0.5	17.2	
4	30.7	−1.6	12.4	
6	34.8	−2.45	17.3	
Average		−0.28	21.21	33.10

APRIL 2, 1909, 9:30 A.M.; ROOM 16.5°

1	44.3°	3.0°	26.9°	......
2	53.3	0.75	36.0	......
3	33.8	0.7	17.9	......
4	30.6	−0.1	12.3	......
6	33.7	−1.1	16.2	......
Average......	....	0.65	21.86	77.09

At this point the experiment was stopped and the flasks emptied. The peas in no. 4 showed practically no molding or fermentation. The odor was entirely pleasant, and the radicles of these germinating seeds were long and fine. Flask 2 was found to contain very rotten peas; the peas in flask 1 were fairly rotten; in flasks 3 and 6 the peas were about equally bad, but decidedly less rotten than in 1. This result agrees with the experience of HANNIG, who says: "Nach Erfahrungen des Referenten kann eine Sterilisirung von Samen durch Schütteln in Sublimatlösung alleine nicht erzielt werden, sondern nur dadurch, dass die Samen zuerst mit verdünntem Alkohol oder ausgekochtem Wasser behandelt werden, um die an den Spalten der Samen haftenden Luftblasen zu entfernen."[5] Only experience led me to believe in the possibility of sterilizing by HANNIG's method. Owing to the long duration of these experiments, complete sterilization becomes as difficult as it is desirable. I find no help in this particular in SCHROEDER's recent paper,[6] although for other plants and for briefer times his directions are most welcome.

Adding together the daily gains in heat, we find that, up to the sixth day, on which more heat was lost by radiation than gained in respiration, there had been liberated 2550 calories which had not been lost or converted into work. On the sixth day 33.16 calories more were lost in radiation (or otherwise) than had been liberated during that time in respiration. But when the experiment was stopped on the seventh day, this loss had been made up, and there had been an average total gain of 2593.63 calories in each flask, after all corrections for absorption of heat by the materials con-

[5] Rev. in Zeitschr. Bot. 1:202. 1909.

[6] SCHROEDER, H., Die Wiederstandsfähigkeit die Weizen- und Gerstenkorns gegen Gifte und ihre Bedeutung für die Sterilisation. Centralbl. Bakteriol. 2:28. 1910.

cerned had been made. This amounted to a gain of 370 calories per day, when the seven days are averaged, or 4.93 calories per day for each gram of peas. The comparative daily changes in room temperatures, flask temperatures, and the number of calories liberated, are shown on the accompanying diagram (fig. 5).

FIG. 5.—Graphic representation of the amount of heat liberated by germinating peas

A comparison of these figures with those of BONNIER's classical paper[7] shows at once that my figures are lower than his. For example, he says (p. 12), "1 kilogramme de graines germant dégage en 1 minute 59 calories." The greatest average gain in heat in my experiment was on the fourth day, in which 923.9 calories were accumulated in 23.5 hours. Calling this 924 calories and 24 hours,

[7] BONNIER, G., Recherches sur la chaleur végétale. Ann. Sci. Nat. Bot. VII. **18**:12. 1893.

we get 8.55 calories per minute for a kilo of peas. But one sees at once that in BONNIER's experiments only short intervals of time were employed (36 minutes for the above quoted experiment), whereas my experiments lasted for nearly or quite one week. In fact, I made no effort to "break the record," and was not aware of the record until I figured my results in order to compare them with BONNIER's. I venture to think, however, that my experiments supplement those of BONNIER by showing the continued liberation and loss of great quantities of heat by germinating peas, and presumably by other plants or their parts, for a time and not merely minute by minute. I need hardly say that the experiment above described in detail is only one of many, the results of which are so similar that it is unnecessary to report them.

The quantity of heat liberated by certain animals

Having some curiosity about the liberation and loss of heat by animals, as compared with plants, I made the following experiments. One was with two salamanders lent me by the Department of Physiology of this University. I put them in separate drained Dewar flasks, and left them for 24 hours in the laboratory. The temperature in the flasks fluctuated with the room temperature, so nearly in the same way as if no animals had been in the flasks, that I did not continue the experiment. I report it with no further comment than this, namely, that the salamanders must have exhaled some warmth, but it was inappreciable.

The other experiment was very striking. Into cotton-plugged drained Dewar flask 14, which weighed 167.2 gr., I put a very lively mouse. The weight at the end of the experiment was 186.5 gr.; therefore, the mouse weighed 19.3 gr. As no excretion, solid or liquid, had taken place during the experiment, whatever loss of weight had occurred was due to exhalation and evaporation only. The thermometer readings for a half hour, beginning at once after putting the mouse in the flask, were as follow, the room temperature remaining stationary at 20° C.

During this half-hour of time, therefore, this mouse gave off by radiation and exhalation an amount of heat sufficient to raise the temperature within the apparatus 13.95° C. As previously stated,

the average of 10 determinations shows that it takes 24.8 calories to raise the temperature of flask 14, with thermometer 6 and a cotton plug, 1° C. Hence the heat ***given off*** by this mouse in 30

Time	Temperature	Time	Temperature
2:30 P.M.	22.6°	2:47.5 P.M.	32.0°
2:34	23.1	2:48	32.2
2:35	24.3	2:48.5	32.4
2:35.5	24.6	2.49	32.6
2:36	25.1	2.49.5	32.7
2:36.5	25.4	2:50	32.9
2:37	.25.7	2.50.5	33.1
2:37.5	26.2	2.51	33.2
2:38	26.4	2:51.5	33.6
2:38.5	26.7	2.52	33.9
2:39	27.1	2:52.5	34.1
2:39.5	27.5	2:53	34.5
2:40	27.9	2:53.5	34.8
2:40.5	28.3	2:54	35.0
2:41	28.7	2:54.5	35.2
2:41.5	29.0	2:55	35.35
2:42	29.2	2:55.5	35.5
2:42.5	29.4	2:56	35.6
2:43	29.6	2:56.5	35.7
2:43.5	29.9	2:57	35.9
2:44	30.1	2:57.5	36.05
2:44.5	30.5	2:58	36.3
2:45	30.7	2:58.5	36.1
2:45.5	31.0	2:59	36.2
2:46	31.2	2:59.5	36.4
2:46.5	31.5	3:00	36.55
2:47	31.7		

minutes amounts to 345.96 calories at least. This takes no account of the amount of heat lost in this time by this set of apparatus, being given off to the air; nor does it include any estimate of the heat retained by the body of the mouse. The body temperature of a mouse I do not know, nor do I know whether the body temperature rose during the experiment. This amount of heat, therefore, is simply what is absolutely lost to the animal, an amount equal to 11.19 calories per minute. The rise in temperature is indicated by fig. 6.

Does the age of the seed affect the heat yield?

I do not know that any successful attempt has been made to answer this question, in spite of the theoretical and practical importance which are evident on a moment's reflection. If the

heat yield bears a fairly uniform relation to the age of the seed, this may be the cause, or it may merely be the reflection or symptom or result of that chain of causes, which finally deprives the seed of its germinating power. Even so, it is important to determine whether this is the case or not. And if it can be shown that the

FIG. 6.—Rise in temperature in flask 14, in which a mouse was confined

heat yield is proportional, or inversely proportional, to the age of the seed, other things being equal, and a convenient method can be employed for determining this, we shall have, for the first time, a means of ascertaining the age and the viability of seeds. Those who have had any experience in buying seed have also known the

disappointment in fine-looking but worthless seed which failed to germinate. The Pure Food and Drugs Act has made it necessary to take fewer articles which come under its operation on faith or on the word of the dealer. But there being no convenient way of testing the quality of seeds, they are as unreliable as ever. It is highly desirable, therefore, from a practical standpoint, to have a method of testing seeds as to their germinating power. Such a method must be reasonably accurate and convenient. I believe it will be found that Dewar flasks may be adapted to this use, and I wish to furnish a certain amount of evidence now in favor of this belief, hoping to be able to determine the matter before long.

Peas retain their germinating power much longer than many other seeds, longer than the ordinary grains, for example.[8] They are even less suitable, therefore, for experimental investigation of this matter than many other seeds. I happen to have in my laboratory, however, peas bought in 1908, 1910, and 1911. Each lot must have been of the preceding year's crop, or older; but owing to the large yearly demand for pea seed, probably very little old stock of this sort is carried over, and I believe, therefore, that the seeds in my laboratory are, most of them at least, of the crops of 1907, 1909, and 1910. The variety is commercially known as "American Wonder," an "extra early." The following table shows the behavior of these three crops in Dewar flasks this year, in constant temperature room A. The flasks and thermometers were sterilized by washing with concentrated aqueous solution of corrosive sublimate, and subsequently rinsed three times with sterile distilled water. The peas were weighed, air-dry, in 80 gr. lots and put, with 100 cc. boiled distilled water, in each of the flasks to be used. The boiled water and the peas, as well as all the parts of the apparatus, were kept in the constant temperature room for at least 24 hours before an experiment was set up. The water was drawn off at the end of the first day.

To this table I should like to add the figures reported in my first paper describing the use of Dewar flasks as respiration calorimeters,[9] for these figures were obtained by using the same 1907 crop of peas.

[8] PFEFFER, W., Pflanzenphysiologie 2[2]: p. 327 and the literature there cited.

[9] PEIRCE, G. J., A new respiration calorimeter. BOT. GAZ. 46:199. 1905.

JANUARY 19–23, 1911; CROP OF 1910

		1st day	2d day	3d day	4th day	5th day
Flask 7.....	17.8°	18.7°	21.8°	27.8°	31.1°	....
Flask 8.....	17.8	18.5	22.3	26.9	31.5	....
Flask 13.....	17.7	18.5	22.4	26.4	33.0	....
Average gain		1.33	4.93	9.8	14.63	....

JANUARY 25–28, 1911; CROP OF 1909

Flask 9.....	17.0°	17.9°	22.7°	25.3°	....	....
Flask 10.....	17.5	18.4	23.7	26.4	....	....
Flask 11.....	17.1	19.0	23.1	24.9	....	....
Flask 12.....	17.0	18.0	24.2	27.9	....	....
Flask 13.....	17.0	19.5	25.15	28.1	....	....
Average gain		1.44	6.72	9.4	....	....

JANUARY 31–FEBRUARY 5, 1911; CROP OF 1907

Flask 10.....	17.2°	17.8°	21.8°	25.8°	29.1°	32.8°
Flask 11.....	17.1	17.8	19.4	23.7	23.6	25.2
Flask 12.....	17.1	17.6	19.3	21.3	23.2	24.4
Flask 13.....	17.2	17.8	22.2	26.8	30.8	35.4
Average gain		0.6	3.52	7.25	9.52	12.3

It should be said that the following temperatures were obtained under the far from uniform conditions of the laboratory, for I did not at that time have a constant temperature room.

APRIL 29–MAY 2, 1908; CROP OF 1907

Flask 1......	22.7°	27.0°	33.4°	36.8°	....	....
Flask 2......	21.6	25.7	35.1	40.5	....	....
Flask 3......	22.1	27.3	35.3	41.4	....	....
Flask 4......	22.4	27.4	35.0	38.8	....	....
Flask 6......	22.3	26.5	34.5	40.0	....	....
Average gain......		5.56	12.44	17.3	....	....

Assuming the correctness of these figures (and both the 1908 and 1911 figures above given are among many that might be given) and making all due allowances for the differences in temperatures between the laboratory and the constant temperature room, one must admit there appears to be a decided difference in the amounts

of heat given off. The flasks used in 1908 were inferior as insulators to those in use in 1911; hence the 1908 figures are not as high as they would have been if more efficient insulators had been employed. So far as these figures show, therefore, it appears that the amount of heat liberated by germinating peas decreases with

FIG. 7.—Heat yields of peas of different ages

their age. If this be true, the amount of heat liberated may then be used as the index of the age or freshness of seeds.

The accompanying diagram (fig. 7) represents the above figures in the form of curves. The difference between the curves of 1907 peas in 1908 and 1911 is even more striking than the figures on which they are based.

It does not by any means follow that the other processes of the

plant decline proportionally with the liberation of heat. Experience shows that old seeds germinate less well than fresh. The foregoing experiments show that the heat yield is less in old than in fresh peas. One record of mine, made up of many measurements, connects growth with these other two processes.

Peas which had been sprouted and kept for four days in Dewar flasks were subsequently put in moist sand to continue germination. The peas were of two lots, those of the 1907 crop and those of the 1909 crop. One week later they were carefully taken up and measured. The average length of the 1909 seedlings was 9.70 cm., of the 1907 seedlings 3.52 cm. The latter is scarcely more than 60 per cent of the former. The seedlings from the older seeds made less than two-thirds the growth of the seedlings from fresher seeds in the same length of time and under the same conditions. The accompanying diagram shows this graphically (fig. 8).

FIG. 8.—Lengths of seedling peas of same number of days' growth, but of different age of seed.

If the result just now described were not consistent with the difference in heat yields according to the age and freshness of pea seeds, I should place no reliance whatever on it. As it is, I do not understand why I did not test such an interesting result by repeated experiment, but I have not yet done so. The question seems to me to deserve further examination.

The possible significance of heat liberation in respiration

From the foregoing experiments, whether on germinating seeds or on warm-blooded animals, it appears that there is a much greater release of energy in the form of heat than can be or is used as such by the organism. Admitting that, under the extraordinary conditions of the experiment, the mouse previously described may not have behaved normally in any respect, and that the production and loss of heat may have been excessive, it is nevertheless evident

that the loss of heat by a warm-blooded animal is very great. When we reflect that all of the heat lost is liberated from the food of the animal, that the loss by radiation will vary with the temperature of the environment and the efficiency of the animal's covering as an insulator, whether this be hair, feathers, subcutaneous fat, or clothing, and that the loss by exhalation will also vary with the rate of exhalation, then we must realize that very much of the heat liberated in respiration is lost. What percentage this is in the case of a mouse I do not know, and it is hardly necessary to know at the moment. It is evident that if the liberation of heat is the essential result of respiration, respiration must be an excessively wasteful process.

Having once conceived respiration to be primarily for furnishing the living organism with energy in the form of heat, I am constrained now to regard it very differently. That it is the chief means of liberating energy still seems to me most probable; but apart from the production and maintenance of a body temperature apparently most favorable to the other functions collectively, the liberation of heat in respiration appears to be wasteful. It may be as useless as it is inevitable.

The material products of respiration vary with the food, with the materials oxidized, directly or indirectly, in the body. Intracellular respiration, or the catabolic processes, the end products of which are oxides and heat, may not only produce within the cell the optimum temperature for its activities and liberate energy at once converted into work, but they may also neutralize (destroy) substances which would otherwise be or become injurious to it. The oxidation of these substances would necessarily be accompanied by heat liberation. The heat thus liberated must be either converted into work or given off, lest again the organism suffer. We may, therefore, conceive the heat liberated in respiration to be of two sorts: a part of it useful in certain organisms, or even certain cells, in maintaining a bodily or cellular temperature which is the optimum or so-called "normal"; and another part, in excess of this first part, which is waste, to be gotten rid of as promptly as any other waste. It is a dangerous product, as the organism in fever shows.

We may, then, regard the end products of respiration, the

oxides and the heat, as wastes. Although inevitable they are not essential; some of them, possibly all, are dangerous, and for this reason to be eliminated as quickly as possible.

The bodies of animals are compact masses compared to the bodies of plants. From the extensive surface of the plant body radiation is rapid; from the limited surface of the higher animals, it is slow. The plant needs no forced draft to carry off its waste heat; the massive animal does. The submersed animal is in a medium which quickly absorbs heat; it needs little else than the water it lives in to relieve it of its waste heat, as well as its waste oxides. Its simple circulatory system is adequate. But air absorbs little heat; it is indeed a fair insulator as compared with water, as the bather in cold water knows by experience.

The liberation of heat may be used, like carbon dioxide, by the physiologist as a gauge of the activity of respiration, but like carbon dioxide, it must be regarded by him as an end product, a waste, and not the essential product. The essential product of respiration may be energy, but if so, it is that energy which is immediately convertible, and is converted into work by the organism. On the other hand, respiration may be essentially a process of purification, in which useless or injurious substances are converted into forms which can be eliminated. The liberation of energy accompanies these oxidations. Some of this energy may be useful and used; much of it is useless and is eliminated. Elimination by radiation is sufficient in organisms of extensive area in proportion to their mass. Radiation is insufficient for organisms of small area in proportion to the mass. In these the circulatory and so-called respiratory systems are employed to eliminate heat as well as the material products.

In this study of heat liberation, therefore, I believe I have been occupied with an unessential, although inevitable, feature of the process of respiration. The essential part of the process of respiration is much more likely to be found to be chemical and not physical. And if this is made any more evident by this study, my work is not in vain.

LELAND STANFORD JUNIOR UNIVERSITY

TYPES OF CUBAN TOBACCO

HEINRICH HASSELBRING

(WITH PLATES IV–X)

One of the most persistent ideas in evolutionary writings which deal with cultivated plants is that transferring a plant from one region to an entirely different one, or from one environment to another, is accompanied by unprecedented variability during the first season of growth after the transfer. The phenomenon is generally described as "breaking up of the type."

When Cuban tobacco seed is grown in the United States, the crop produced is not uniform, but consists of a mixture of many different forms. SHAMEL,[1] who has made extensive experiments with the introduction of Cuban tobacco into the United States, describes this phenomenon and attributes the appearance of a diversity of forms from the imported seed to the variability induced by the new environment. Regarding the variability of plants from seed imported from Cuba and Sumatra, SHAMEL and COBEY[2] say:

> The plants grown from this freshly imported seed broke up into many different types. . . . . This breaking up of type is due to the effect of the change of soil and climatic conditions, resulting in striking variation in the plants grown from the imported seed. The variation is particularly marked where southern seed is taken to northern tobacco districts.

Similar views are expressed in the older literature. Thus LOCK,[3] speaking of the importation of Havana tobaccos into other countries, says:

> There is no great difficulty in raising plants of these varieties, but they speedily degenerate and form new varieties, if the climatic conditions, etc., are not favourable.

[1] SHAMEL, A. D., The improvement of tobacco by breeding and selection. U.S. Dept. Agr. Yearbook 1904:435–452. *pls. 7. figs. 2.*

[2] SHAMEL, A. D., and COBEY, W. W., Varieties of tobacco seed distributed in 1905–1906, with cultural directions. U.S. Dept. Agr., Bur. Plant Ind. Bull. 91. pp. 38. *pls. 9.* 1906.

[3] LOCK, C. G. W., Tobacco: growing, curing, and manufacturing. London. 1886. pp. 32.

Recently similar phenomena have been described by COOK[4] and his collaborators as occurring in cotton when transplanted from one locality to another. It is evident from these citations that it is a common belief that plants, when transported from one environment to another entirely different one, tend to break up into a number of new types. This view is held by many writers, especially regarding tobacco.

During the years 1907 to 1909, while connected with the Cuban Experiment Station at Santiago de las Vegas, I was able to gather a number of facts and to carry out some experiments which lead to a different interpretation of the phenomena observed when Cuban tobacco seed is imported and grown in the United States. The results of these observations and experiments are given in this paper. For a complete understanding of the phenomena in question, three phases of the subject are considered: (1) the composition of so-called Cuban tobacco; (2) the special methods of agriculture which tend to influence or maintain the present composition of Cuban tobacco; and (3) cultural experiments with types of Cuban tobacco.

The composition of Cuban tobacco

Even a casual survey of the tobacco fields of western Cuba shows that the crop in any field lacks entirely that uniformity which is characteristic of any field of plants of one variety in regions of more advanced agriculture. The plants show a great variety of forms, which at first seems bewildering. Upon closer study, however, it is seen that some types predominate. Most of the plants may be divided into groups, the members of which resemble each other more or less. It is impossible, however, to delimit such groups definitely, or to class all the plants into groups by a taxonomic study. Certain types are well marked, but the number of minor forms, differing in width and length of leaves, habit, branching, etc., is so great that the whole appears to be a mixture of innumerable intergrading forms. While, as has been stated, some of

[4] COOK, O. F., Local adjustment of cotton varieties. U.S. Dept. Agr., Bur. Plant Ind. Bull. 159. pp. 75. 1909.

COOK, O. F., MCLACHLAN, A., and MEADE, R. M., A study of diversity in Egyptian cotton. U.S. Dept. Agr., Bur. Plant Ind. Bull. 156. pp. 60. *pls. 6.* 1909.

the forms occur with great frequency and form the predominating elements of the mixture, others are rarer, although distinctly marked. Some of the more striking forms can be recognized and described taxonomically, but for the majority of the intergrading forms cultural work is necessary in order to determine their constancy. The condition here described exists, so far as I have been able to determine by examination of the fields or by growing seeds from different sources, in all the tobacco fields of western Cuba, or the regions known as the Vuelta de Abajo and the Partidos districts. It is not likely that the tobacco fields of the eastern district will be found to differ in composition from those of the other regions. The condition shows that there has been no systematic effort directed toward the amelioration and improvement of the tobacco plant in Cuba. The persistence of the present condition is explained by the special methods of agriculture in vogue in Cuba.

Methods of agriculture

In the regions of Cuba which have been long under cultivation, great difficulty is experienced in growing *posturas*, or young tobacco plants. The soil is so thoroughly infected with fungi that a rain at any time during the season for growing *posturas* is sure to result in the entire destruction of the plants in the seedbeds. I have seen many acres of seedbeds in the finest condition destroyed in a few days by fungi following a heavy rain. As a result of this, it is customary to grow a large part of the *posturas* in the newer lands in the mountains, in soil which is partly sterilized by burning brush on the surface. The *posturas* are tied in bundles, which are packed in large bales and sent to the various tobacco districts of the island. Any grower who has lost his *posturas* makes up the supply by purchase from the mountain growers. Many growers depend entirely on these mountain-grown *posturas*, seed for which is gathered in various parts of the island. Whether the grower is gathering seed for sale or for his own use, no attempt is made to select seed from the best plants. All the plants in the fields are topped and harvested. It is not even customary to allow any of the plants to flower on the main stem and produce seed. After the harvest of the leaves, the stems are cut off close to the ground,

and the field is abandoned, receiving no further irrigation, which is necessary during the growing period of the crop. As a rule, there is sufficient moisture in the soil to produce a crop of suckers from the old roots. These make a weak growth among the weeds of the abandoned fields and produce flowers and seeds. It is this crop of suckers which furnishes the seed supply for the new crop of tobacco.

Under these conditions, any form of selection is impossible, for the sucker shoots do not show the characteristics of the parent plant. When the seed is mature, all forms, good and bad, are indiscriminately gathered and resown the following season.

These methods of obtaining seed and growing *posturas* bring about two results: (1) all types of tobacco that occur in Cuba are maintained there by the blanket method of harvesting seed indiscriminately from all kinds of plants; and (2) by reason of the traffic in *posturas* and seeds, all types are distributed to all the tobacco-growing regions, so that a uniform mixture of types is maintained over the island.

Cultural experiments

As has been stated, a study of the plants in the field is not sufficient to disentangle the mixture of types and lead to exact information regarding their constancy. To determine whether these types are constant, or whether Cuban tobacco possesses the enormous variability usually attributed to it, cultural experiments were begun in 1908. During the tobacco season of that year, about 30 plants were selected which seemed to represent distinct types. A careful description, recording all characteristics that might be of any value in identifying the types, was written for each plant. The plants were staked and labeled and given a number. Inasmuch as the plants had been topped, it was necessary to save seed from the suckers which appear at the base of the plant after the stem is cut. A number of the plants did not form suckers, so that only 14 plants remained. The suckers selected for seed were inclosed in manila bags in the usual way, while the others were cut as soon as they appeared. In this way, guarded seeds from 14 isolated, self-fertilized mother plants were obtained.

In harvesting and separating the seeds from the capsules, of course every precaution was used to avoid mixing the different types. Each bag was taken separately and the seed shelled out in a large porcelain evaporating dish in the laboratory. The different lots were handled in such a way that there was no possibility of a stray seed being blown or scattered among those of another lot.

Similar precautions were used in sowing the seeds the following autumn at the beginning of the next tobacco season. The seeds were sown in flats, in soil taken from a nursery where no tobacco had been grown, and distant from any tobacco field. The soil was sterilized with hot water. After the seeds were sown, the flats were covered with burlap frames, and were protected from ants, which carry off the seeds, by a ridge of powdered naphthalene around the edge of each flat. The posts supporting the benches on which the flats stood were kept wrapped in cloth soaked in crude oil. The benches had been previously freed from ants by boiling water. With these precautions, no trouble was experienced from the insects. The flats were kept in an open shed.

The seeds were sown September 16 and 18, 1908. When the seedlings were large enough, they were pricked out in open frames kept covered for a time with canvas. The *posturas* were planted in the field at various times from November 12 to December 9, 400–500 plants of each type being set out.

The results of the cultures were so striking and uniform that they can be stated in a few words. Even in the open frames the various groups of plants showed differences which made them stand out from each other, but the differences were more evident when the plants were mature. The descendants of each plant were entirely uniform and like the parent plant from which they were derived. Even minute and unimportant characters were transmitted with surprising definiteness.

While the different types were indiscriminately intermingled in the field, the contrast even among extreme types was obscured on account of the many apparently intergrading variations, but in the cultures where large numbers of each type were grouped together the differences were unmistakable. Thus, for instance, the different groups as a whole showed marked differences in height,

a characteristic which was not evident in the field, where owing to individual variation the stature of a plant is not a pronounced characteristic. Yet when the descendants of individual parent plants were brought together in groups under uniform conditions, the contrast in stature between the different groups was constant and very marked.

The more important morphological characteristics in which the various types differed from each other were the shape of the leaves and flowers, and the form of the inflorescence, but the descendants of a single parent were entirely uniform with respect to these characteristics. Even such minor characteristics as the tint of the leaves and color or shade of the flower were uniform throughout the plants of each group. In some cases the same type had been selected more than once, so that some of the groups were identical. The plants in the field were studied during their entire growing season, and each individual was often examined, but among the several thousand plants no aberrant form occurred.

The uniformity of the descendants of each of the parent plants indicates that the plants originally selected represented elementary species, for if the parent plants had been hybrids, splitting according to Mendel's law, the splitting should have occurred in the generation of 1909. The absence of hybrids among the plants selected can be explained by the ease with which self-pollination takes place, and by the scarcity of pollinating insects. The flowers are slightly proterogynous, but even before the flowers are fully open the anthers begin to shed their pollen. As both pistils and stamens are about equal in length, self-pollination is easily accomplished. Pollinating insects seem to be rare. During the two seasons in which I spent much time in the tobacco fields, I observed only in a few instances honey bees and hawkmoths pollinating flowers. It seems very likely, therefore, that in the majority of cases the tobacco flowers in Cuba are self-pollinated.

In order to continue the pure line cultures, a large number of plants of each type were bagged for seed in the usual way, but on account of my removal from Cuba in the spring of 1909, seeds from all the types were not obtained. Some clusters with mature seeds were found on 11 of the types. The seeds from 10–15 plants of

each of these types were collected and brought to the United States. These seeds were grown at Flint, Mich., during the summer of 1910.

It is in the first crop from seed imported from Cuba that the splitting of the type into numerous varieties has often been reported. The plants in the pure line cultures in Michigan, however, showed no signs of such splitting. The plants resulting from the mixed seed of 10–15 plants of each type were entirely uniform and similar to each other. In all their important morphological characteristics they were identical with their parent plants grown in Cuba the year before. In some minor characteristics some types differed from the plants grown in Cuba. The leaves were of a darker green and the plants generally were taller and more vigorous in the more fertile soil of Michigan. In so far as there was any detectable influence due to the new environment, all the plants of a particular type reacted alike.

Discussion

It appears from the foregoing experiments that when pure strains of tobacco are selected from the mixture grown in Cuba and brought into a new environment in the United States, these pure strains show no breaking up of the type due to the new environment. The slight changes which are observed in the plants affect all the plants of one type alike.

The effects observed by Shamel and Cobey and others are attributable to the fact that the seed was derived from a mixture of types. Since a great number of types occur in the fields of Cuba, it is not necessary to invoke the doctrine of "breaking up of types" to account for the appearance of numerous varieties when Cuban seed is sown in the United States.

The same principle applies to tobacco and other plants cultivated in countries where agriculture has not reached a high state of development, and where the concept of an agricultural or horticultural variety hardly exists. In Cuba I have cultivated tobaccos from a number of districts in Mexico, and find that these are also mixtures of types which resemble in their general appearance the Cuban types and probably belong to the same group of elementary

species. Recently HOWARD and HOWARD,[5] in their excellent studies on Indian tobaccos, have isolated 51 types from the tobaccos grown in India, and have shown that these types remain constant even in minute and insignificant characteristics when propagated in pure line cultures. SHAMEL[6] also has found and repeatedly emphasized the fact that when seed is obtained from single self-fertilized mother plants, the progeny is entirely uniform. In one instance he reports that plants from Florida-grown Sumatra seed showed great variability for two generations when grown in Connecticut, the seed being collected in the ordinary way from many plants, but when seed was saved from single mother plants in the second generation of northern grown plants the offspring of these plants were uniform. The variability continued for two generations,

s collected from isolated plants the environment
ect!

n exactly analagous behavior in cotton. When
om individual mother plants selected from the
King cotton grown at San Antonio, Tex., the
orms were either uniform or showed definite types
e occurrence of definite types of variation would
hat the parents were hybrids.

elievable in either the case of tobacco or of cotton
tion would destroy the plant's capacity for being
environment. In tobacco variation has been
st at least during two generations in the new
from individual plants selected at any time a
obtained. All such facts are more easily under-
s that the seed was derived from mixed parents.
urse, that plants are modified in their fluctuating
changes in the environment, but so far as experi-
hows, such modifications persist only as long as
nducing them persists. LE CLERC and LEAVITT,[8]

HOWARD, G. L. C., Studies in Indian tobaccos. Mem. Dept.
3:59–176. *pls. 58.* 1910.

oc. cit., Yearbook. 1904. [7] COOK, O. F., *loc. cit.*

, and LEAVITT, S., Tri-local experiments on the influence of
nposition of wheat. U.S. Dept. Agr., Bur. Chem. Bull. 128.
OT. GAZ. 50:153. 1910.

in their work with wheat, showed that this influence of the environment is exerted also on the chemical composition of plants. When wheat of one variety from one locality was grown in other localities, with a widely different environment, the chemical composition of the grain was different in each locality. These differences persisted as long as the wheat was grown in the particular locality, but if at any time seed from one locality was grown in any of the others, the grain took on the composition of the wheat constantly grown in those localities. The tobacco plant is extremely susceptible to changes in the environment, but such changes affect all the plants of a pure strain alike, and do not cause a breaking up of the type. Among the plants grown in Michigan, some of the types showed a different shade of green from that shown by the same types in Cuba, but all the plants changed alike.

Description of the types

The taxonomy of the TABACUM section of the genus *Nicotiana* is endlessly confused, and it is not possible from the materials at hand to give a proper classification of the forms involved in these studies. Many of them are undoubtedly well defined species. The facts that they have maintained themselves for a long period of time, that no effort has been made to improve them, and that they resemble races from Mexico, seem to indicate that these forms are not far removed from the original wild species of tobacco. As their definite classification would require the study of vastly more material than is at my disposal, it seems best to indicate the general relationships of the types and give the main characteristics by which they were distinguished. For similar reasons, it is useless to speculate on the origin of the forms of tobacco which now occur in Cuba. Many of the growers have a vague idea that the tobacco of today is not the real Cuban tobacco famous in former times. It is a common belief among them that during the long wars tobacco growing was almost exterminated on the island, and that subsequently tobacco was imported from Mexico, Porto Rico, and other regions. It is more probable, however, that even in early times the tobacco of Cuba consisted of a mixture of forms. As early as

1722, LABAT[9] describes four forms cultivated on the islands of tropical America, and it is quite probable that these were generally distributed over the islands.

In the following pages a brief description and history of the 11 types cultivated both in Cuba and Michigan are given. In designating the types, the same numbers are used by which they were designated in the cultures. In the accompanying plates showing leaves of the different types, each type shown is represented by all the leaves of a single plant of that type.

Broadly speaking, the types may be divided into two groups. The plants of the first group are characterized by broad, rounded leaves, short in comparison with their width, and scarcely or not at all pandurate, but sessile by a broad base and decurrent auricles; or the lower leaves contracted into a somewhat pandurate shank. The base or shank of the leaves in general is not as much wrinkled as in the second group. The upper small leaves on the stem and subtending the branches of the inflorescence are ovate, acute, or barely acuminate. The corolla tube is suddenly inflated just above the middle, and the limb is pentagonal and obscurely or scarcely lobed, the lobes being apiculate. The plants of this group probably constitute the collective species *Nicotiana macrophylla*. The group will therefore be referred to as the *macrophylla* group.

The plants of the second group are marked by oblong-ovate leaves, longer in comparison with their width than those of the first group. They are more pointed, often acuminate, and have the base contracted into a pandurate, very wavy and wrinkled shank, with broad, decurrent auricles. The uppermost leaves are ovate to lanceolate and long-acuminate. The corolla tube is trumpet shaped, gradually expanding from the base, with the stellate limb distinctly and often deeply lobed, with sinuate-acuminate lobes. This group is more heterogeneous than the former, and makes up the greater part of the tobacco grown in Cuba. The typical forms of this group probably constitute the collective species *Nicotiana havanensis*. Some of the less typical forms may belong to others of the older species.

[9] LABAT, JEAN BAPTISTE, Nouveau voyage aux isles de l'Amerique. 4to ed. 2:166. 1724; also 12mo ed. 4:476. 1724; the edition of 1722 was not seen. See also Du Tertre Jean Baptiste Histoire générale des Antilles. 2:99. 1667.

THE MACROPHYLLA GROUP

No. 7: pl. IV. fig. 1; pl. VI. fig. 7; pl. X. fig. 14

No. 7 is a dark green vigorous type which grew to a height of 2 m. in Cuba and 2.5 m. in Michigan. In the field growing near the other plants of the *macrophylla* group, the plants of this type stood out in strong contrast by reason of their darker color and tall growth, and their loose spreading inflorescence. The leaves are rather thick and firm in texture. This type is not liked by Cuban growers, some of whom saw it in the experimental plats.

Nos. 16 and 28: pl. VII. fig. 9

Nos. 16 and 28 proved to be identical. They are a broad-leaved type, differing from no. 7 in their dwarfer habit and more compact growth, as well as in their paler green color. The whole inflorescence is more compact than that of no. 7, and the flowers are paler. When grown side by side, these two types show a uniform and striking contrast with no. 7.

No. 18: pl. IV. fig. 2; pl. VIII. fig. 11; pl. X. fig. 15

No. 18 has the general habit and characteristics of nos. 16 and 28, which it resembles more than it resembles no. 7. This type is distinguished from the others by its remarkably large broad leaves, which are soft and flaccid, so that they appear wilted in the sun. Some plants of this type grown in Cuba during the summer season showed all the characteristics of the parent plants which had been grown during the previous winter. In Michigan the leaves grew to a very large size, but remained soft and flaccid, differing clearly from the more turgid leaves of the other forms.

THE HAVANENSIS GROUP

No. 25: pl. IV. fig. 3; pl. VIII. fig. 10; pl. X. fig. 17

No. 25 has broadly ovate or oblong leaves, arching at first and later deflexed, narrowed into a distinct pandurate, wavy, and bullate shank, which expands again into large wavy auricles terminating in long decurrent wings. The upper leaves are ovate to ovate-lanceolate and acuminate. This form may be taken as

typical of the bulk of the tobacco grown in Cuba. By far the greater part of the plants in the fields belong to this type, and differ from the particular strain here described only in minor details, such as shade of the flowers, length and breadth of the leaves, and height of the plants. These minor variations, however, seem to be transmitted with great fidelity in strains descended from a single plant. Cuban growers who saw the plats uniformly picked out such types as this and nos. 36 and 37 as *Tabaco criollo*, which signifies that it is the pure Cuban. The broad-leaved types, as well as the narrow-leaved forms mentioned farther on, were generally regarded with disfavor by the Cuban tobacco growers. From these facts it seems probable that this type represents the typical Cuban tobacco cultivated in the early history of the Island and known in horticulture as *Nicotiana havanensis*.

Nos. 36 and 37

These two forms are also typical Cuban forms and differ from no. 25 only in the width and length of the leaves. The difference in width of leaves of the different strains, while very slight, was still apparent when the plants stood in groups side by side. Too much stress should not be laid on differences of this nature unless accompanied by other characteristics, or unless the differences can be clearly defined by plotting the variability curves. For all purposes, except those having in view the selection of superior strains, these types can be grouped with no. 25 as typical Cuban or Havana tobacco.

No. 12: pl. V. fig. 4; pl. VII. fig. 8; pl. X. fig. 18

No. 12 is a Cuban type, but differs from the foregoing forms in several ways, so that it was readily distinguished. The leaves were thicker, more rigid, and narrower than the other forms. In Cuba the leaves had a peculiar gray-green color which contrasted sharply with the neighboring plants. In Michigan this difference in color was less conspicuous, but all the plants of this type reacted alike as to the loss of color. The flowers are deep rose. On account of the stiffness of the leaves, their distance on the stem, and the smallness of the upper ones, the plant has an open habit quite distinct from the larger-leaved types.

No. 5: pl. X. fig. 16

No. 5 is a Cuban type with unusually broad leaves, which are obtusish at the apex, and with the shank not so distinct as in the other types. The form tends toward the broad-leaved types. The flowers are white or very pale pink, with the limb of the corolla lobed as in the other Cuban types. The plants retained all their characteristics in Michigan.

No. 32: pl. V. fig. 5; pl. IX. fig. 12

No. 32 is striking on account of its strict habit and peculiar deep bluish-green color. The leaves are of the narrow type, oblong to oblong-ovate, erect, forming an acute angle with the stem, and with the apex long-pointed and arching. The surface is marked with furrows and the pandurate base is much wrinkled. The flowers are deep pink to pale pink, with triangularly lobed limb. The strict habit and thick leaves of dark bluish-green color make these plants very conspicuous in the field. The characteristics of the plants were retained in Michigan.

No. 1: pl. V. fig. 6; pl. IX. fig. 13; pl. X. fig. 19

All through the Cuban tobacco fields there occur narrow-leaved forms which resemble the ordinary Cuban types to some extent, at least while they stand intermingled with them. It is all the more difficult to separate these forms definitely because a number of gradations occur from very narrow leaves to much wider-leaved forms approaching the typical Cuban tobacco. These forms do not constitute a large percentage of the tobacco crop. They are sufficiently conspicuous, however, to have attracted the attention of Cuban growers, who call such forms *lengua de vaca* or cow's tongue. A number of such forms varying in width of leaves were selected, but seeds were obtained from only one form. The others failed to produce suckers. No. 1 is a conspicuously narrow-leaved form. The plants are of dwarf habit, having the large leaves low down on the stem, thus giving the upper part a naked appearance. The leaves vary from oblong-pointed to lanceolate-acuminate. The surface is wavy, being obliquely furrowed parallel to the veins. The base is narrow-pandurate with decurrent

auricles. Inflorescence loose, open. Limb of the corolla deeply lobed, with ovate or triangularly acuminate lobes. Color pale rose to deep rose. In Michigan the form retained the same dwarf habit, with the large leaves on the lower part of the stem. The only difference was that the plants grew more vigorously and had larger leaves in the northern habitat. Types like this and no. 32 differ very conspicuously from the other members of the *havanensis* group, and it is possible that they belong to other species.

Conclusion

The tobacco grown in Cuba consists of a mixture of a large number of forms which maintain their characters from generation to generation. Pure strains, breeding true to type, can readily be selected from this mixture. When such pure strains are grown in northern climates, they do not break up into a number of new types, but the plants of each strain remain uniform. Such modifications as appear, appear alike in all the plants of a given strain.

Bureau of Plant Industry
Washington, D.C.

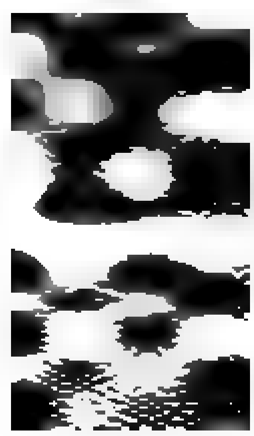
4 5

HASSELBRING on CUBAN TOBACCO

5

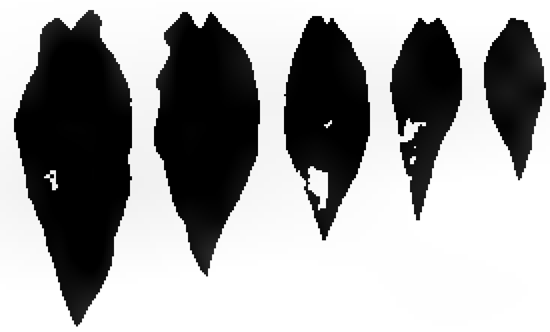
6

HASSELBRING on CUBAN TOBACCO

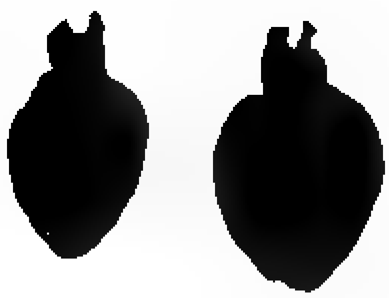


1

HASSELBRING on CUBAN TOBACCO



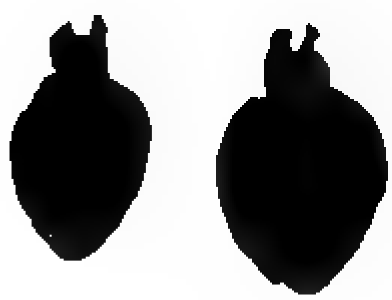
8

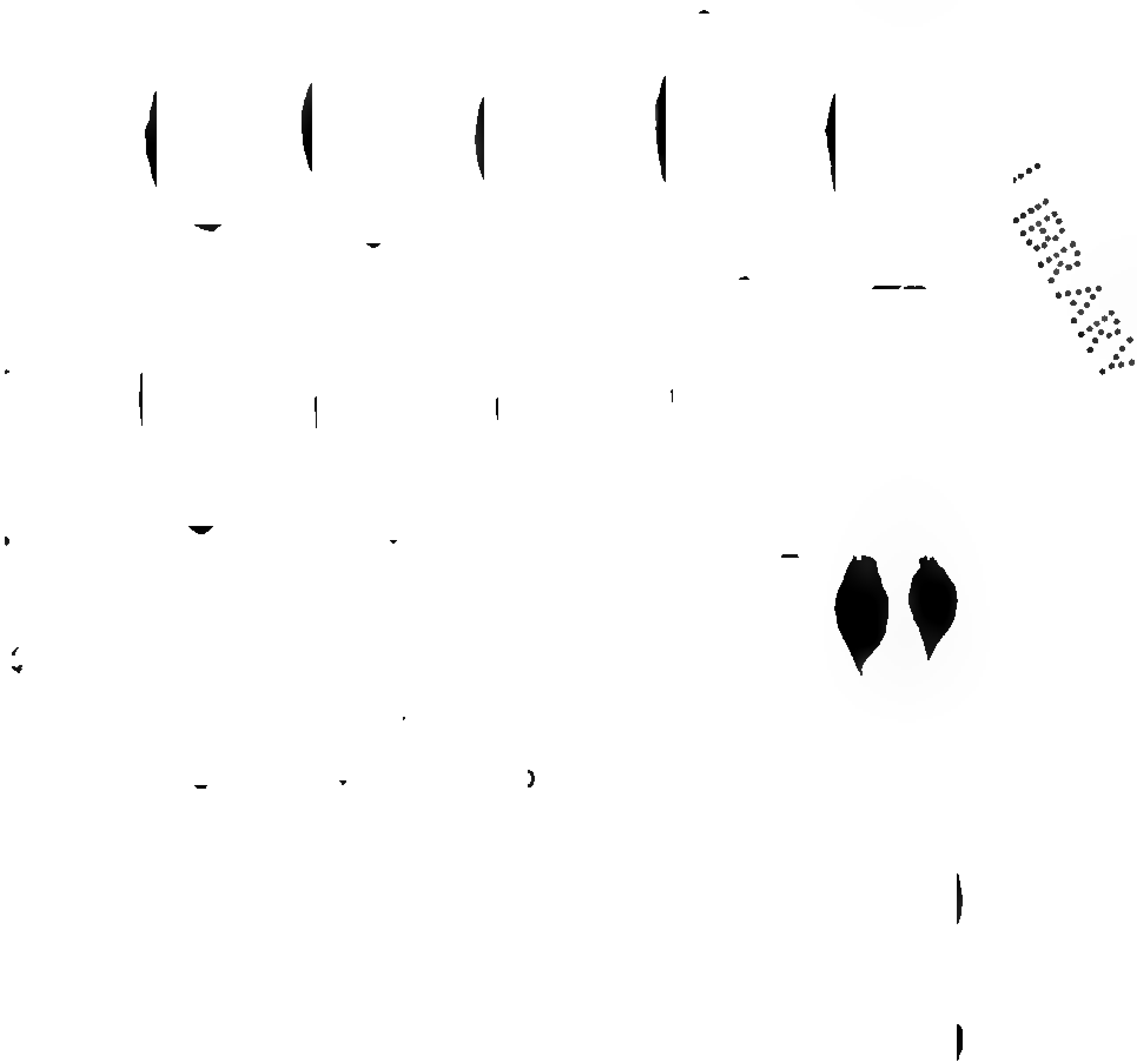


9

HASSELBRING on CUBAN TOBACCO

8

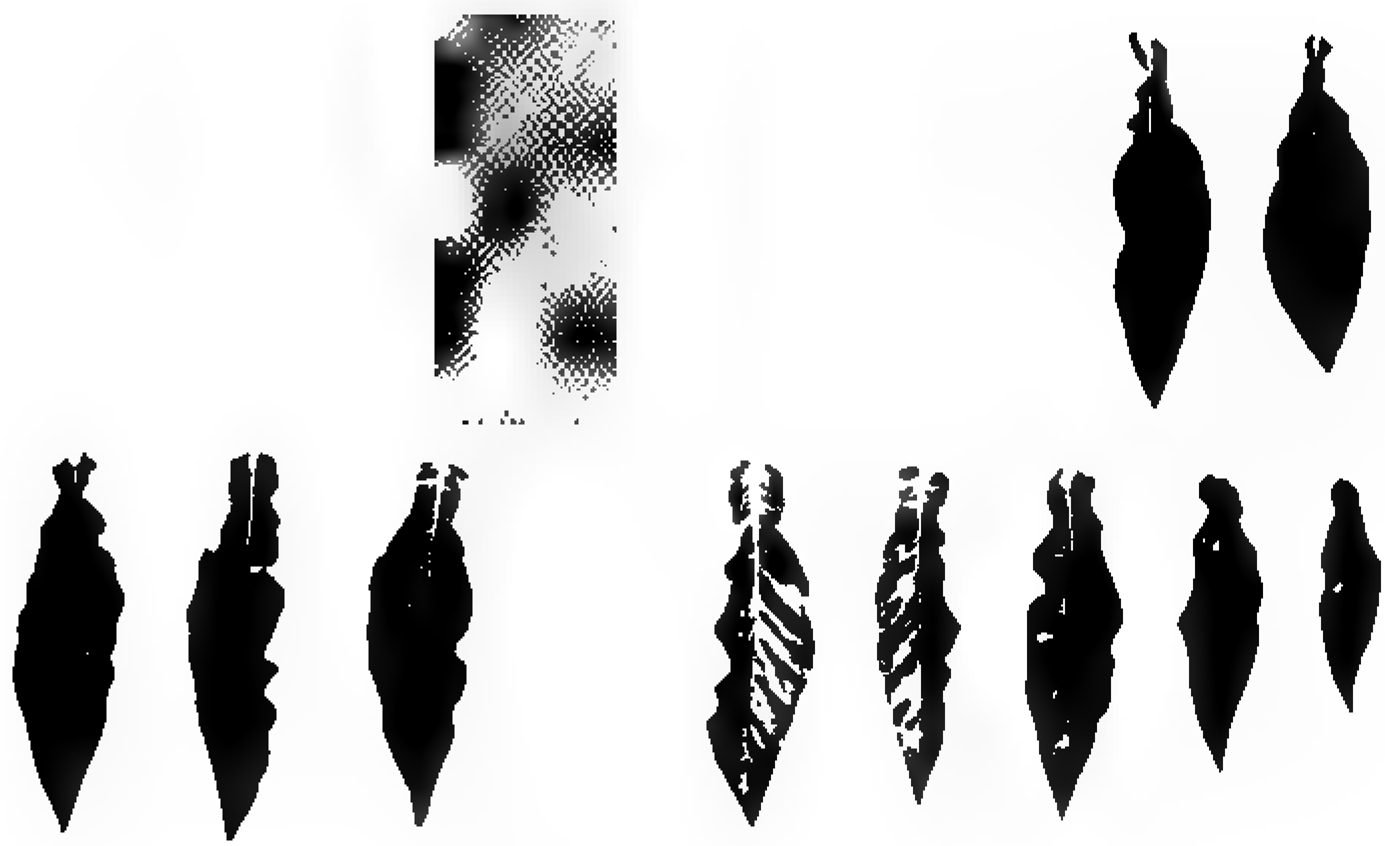




11

HASSELBRING on CUBAN TOBACCO

12



13

HASSELBRING on CUBAN TOBACCO

14

17

15

18

THE DEVELOPMENT AND CYTOLOGY (
RHODOCHYTRIUM[1]

ROBERT F. GRIGGS

(WITH PLATES XI–XVI)

To the student of phylogeny, whether he be taxo morphologist, no organisms are as interesting as those wh to occupy positions intermediate between the larger g help to fill the gaps in our evolutionary system. Su is *Rhodochytrium*, for it seems to occupy a transition between the protococcoid algae and some of the chy fungi. It was described by its discoverer as an alga, bu chlorophyll and is strictly parasitic in its mode of life, bei moreover, to definite host species. Although entirely in photosynthesis, it develops abundant starch. But t grains are apparently built up directly in the cytoplasm, plastids nor pyrenoids have been found. This parado bination of characters aroused in the writer a desire to t the details of its structure and to compare its cytology of *Synchytrium*, which has proved so peculiar.

As is well known, *Rhodochytrium* has been found onl widely separated regions. LAGERHEIM observed it in m in Ecuador on *Spilanthis* sp., and his material has been (in WITTROCK and NORDSTEDT'S *Algae Exsiccatae* as BARTHOLOMEW discovered it on *Asclepias pumila* abou from Stockton, Kansas, and distributed it as *Fungi* (no. 2166 (forma *asclepiadis* Farlow); and finally STEVENS have found it on *Ambrosia artemisiifolia* in many place Carolina, as reported by ATKINSON (3). BARTHOLO informed me that the plant is rare in Kansas and kno from only one locality, but both in Ecuador and Nortl

[1] Contribution from the Cryptogamic Laboratory of Harvard U LXV.

[2] MR. HALL has also found it at Clemson, South Carolina.

it is widely distributed and common. It is in each case, however, except possibly in Kansas, closely limited to the particular host on which it was reported.

The parasite attacks all the aerial parts of its host, but, like certain species of *Synchytrium*, it is largely confined to the tissues immediately adjoining the vascular bundles. To the naked eye each parasite appears as a small bright red spot buried in the tissue of the host. When a piece of the infected tissue is examined under the microscope, it may be seen that the parasites are of two sorts, resting spores and zoosporangia. The resting spores are somewhat deeply buried in the tissue of the host, but their superficial origin may be demonstrated by the persistence of the original germ tube with its external button, *Cystenhäut* (fig. 4), through which the parasite penetrated the host. The zoosporangia (fig. 28) are irregularly turbinate or retort-shaped bodies with wide flaring necks, through which their contents are emptied at maturity as biciliate zoospores which spread the infection during the growing season. From the basal portions of both sorts of cysts numerous rhizoids are given off, which penetrate the vascular bundles of the host, especially their phloem elements, and gather nutrient for the parasite.

In carrying out the investigation I have been aided to an unusual degree by my friends. I desire to extend my thanks and acknowledgments to Messrs. F. L. STEVENS and J. G. HALL of the North Carolina Experiment Station for the material, especially to the latter gentleman, who has put himself to no little inconvenience in killing material at all hours of the night as well as in seasons of the year when it was difficult to secure; to Professor GEORGE F. ATKINSON, who himself planned to make detailed studies upon the plant, for the generous way in which he encouraged me to proceed with the present investigation; and to Professors ROLAND THAXTER and W. G. FARLOW for the courtesies of their laboratory and for much valuable criticism and advice.

The material was killed at Raleigh in chromacetic acid and shipped to Columbus in the killing fluid, after which it was dehydrated and imbedded in paraffine in the usual way. The safranin-violet combination proved most satisfactory as a stain. Iron

haematoxylon, for some reason, was hard to handle with this material.

Observations on living material

Through the kindness of Mr. HALL, supplies of infected ragweed were sent to me at frequent intervals. By this means it was possible to determine the approximate sequence of events through the year. It would be interesting to compare the seasonal cycle of the parasites in North Carolina and in Ecuador, but LAGERHEIM has left us no data concerning the seasonal history of his plant. In regard to the characters of the living cysts and the behavior of the zoospores, I cannot add in any important particular to LAGERHEIM's account, though my observations confirm his at almost every point.

According to my observation, the parasite does not appear at Raleigh until rather late in the season. Seedling ragweeds, gathered among the stubble containing the old resting spores on April 20 and May 20, showed no infection on arrival in Columbus, and did not subsequently develop any when grown in the greenhouse. Young plants gathered May 31, however, showed a few parasites. At first nearly all of the cysts become zoosporangia, but before June has passed, resting spores begin to appear in numbers, the zoosporangia become gradually scarcer and scarcer, until finally, about August 1, practically the only cysts found are the quiescent resting spores which undergo no further change until the following spring. These are even more conspicuous than the zoosporangia, but for any observations, either biological or cytological, material must be gathered while zoosporangia are still abundant, that is to say before the middle of July, preferably during the latter half of June.

With a little care the two sorts of cysts can be distinguished in the living state under a hand lens. The resting spores are more regular in shape and more deeply buried than the zoosporangia, and they are usually more deeply pigmented, since their protoplasm is more compact and less vacuolate.

The first infections observed were mostly on early leaves, which soon wither and drop off in the natural development of the plant,

whether parasitized or not. But before these leaves wither, the parasites they contain ripen and discharge their zoospores, which carry the infection to the younger parts nearer the growing point of the host. In this manner infection is carried to successively higher and higher levels of the growing plant, until the host is often red with parasites.

LAGERHEIM believed that the cysts arose not only by direct infection but also by proliferation from the mycelium of old ones. If this occurred, a single infection might, by repeated proliferation, infect every part of the host plant. But in the form on *Ambrosia* no indication of such proliferation was found. Nowhere among the rhizoids were any indications observed of the formation of new growing points or other signs of proliferation. During the whole of the growth period the parasite is strictly unicellular, with a single nucleus in the body of the cyst, and when nuclear division begins preparatory to sporulation, the nuclei do not wander into the rhizoids. In sectioned material only a small proportion of the parasites are so oriented that a single section passes centrally through the whole cyst. But in no case, where the series was complete, was there any difficulty in finding the external opening of any zoosporangium, whereas if proliferation had been occurring, numerous partially formed cysts which had not yet grown out to the epidermis should have been encountered. In those parasites which become resting spores the independence of the cysts cannot be demonstrated by finding their external openings, because, on account of the narrowness of their necks, only a small proportion of them can be followed to the exterior. If proliferation occurred, the new cysts could become nucleated only by migration of nuclei through the rhizoids. But not only do the nuclei of the resting spores remain undivided, but they have not been seen to wander from their central position in the middle of the cyst, and they are so large that it is difficult to imagine them squeezing through the rhizoids.

Although the parasites are so abundant as almost to cover the host plant, and the rhizoids destroy the cells which they penetrate, the vigor of the plant is little impaired. But when infected ragweeds are transplanted, it is difficult to prevent the parasitized

leaves from withering and dying, and reinfections on healthy portions of the plant are difficult to secure.

The most convenient way to obtain the zoospores is to tease to pieces fragments of tissue containing the cysts, liberating the zoospores by rupturing the sporangia. It is difficult to observe the normal exit of the zoospores on account of their minuteness as compared with the massive tissues from which they emerge. But with patience one can study the discharge. LAGERHEIM states that the plug of the zoosporangium is dissolved before the escape of the spores. In only one case was I able to observe the discharge under satisfactory conditions, and then I saw neither the fate of the plug nor the very beginning of the discharge. The whole mass of zoospores appeared to expand as swarming began, and those nearest the opening were forced out in a solid stream by the pressure of those below them. In the case observed they continued to escape at the rate of about 150 per minute for 10 minutes (that is, approximately 1500 spores). The last ones from the rhizoidal end of the sporangium were not at first so well formed as the others, and did not escape with them, but after an interval of 5 minutes began to swarm violently inside the sporangium and some of them escaped one by one. Not all of them were able to find the opening, however, and those which failed became quiescent after about 15 minutes.

Along with the ripe zoosporangia many immature ones, of course, are torn open in teasing apart the material for mounting. Such of these as have advanced far, though not yet mature, are apparently able to form zoospores under the stimulus of rupture. When first discharged the contents of these cysts undergo euglenoid contortions, but in a few minutes become ciliated and break up into spores. Such zoospores, however, are very irregular in size, and abnormal forms compounded of several individual spores are common. Among these are some which might easily be confused with conjugating gametes, being associated in pairs side by side. More commonly such double zoospores are joined at their posterior ends, forming much elongated bodies, pigmented and ciliate at both ends. Frequently a third member is attached to the middle of such a couple, forming a projection at right angles. Others are

large multiple bodies with four or more pigmented areas and many cilia. Such abnormal spores, of course, have very erratic and peculiar movements. Their period of activity is short, few continuing to swim actively for more than half an hour. LAGERHEIM observed these same abnormal spores, and inferred from them that segmentation was successive rather than simultaneous, but, as will be seen, this is not the case.

The zoospores are transparent, except at the anterior end, which is occupied by a mass of pigment. After they come to rest the nucleus can be seen distinctly as a clear central vacuole. In the posterior portions are numerous granules, usually including some starch grains. When moving most actively, the zoospores are oblong rather than pyriform, as figured by LAGERHEIM. Indeed, they appear to be narrower in the region of the nucleus than in the anterior pigmented end. But this is believed to be due to an optical illusion, the more conspicuous region irresistibly appearing larger. It is of course not susceptible of careful observation, since the shape changes at once when they come to rest.

If plentifully supplied with fresh water, the zoospores continue to swim about actively for several hours. In numerous instances they were watched for half a day at a time, and in one case the last one on the slide did not perish until 8 hours after liberation. In preparations supplied with abundant water conjugation occurs but seldom, according to my experience. But when the water has evaporated to a considerable extent, all begin to conjugate at once. When more water was added, those pairs in which fusion had not proceeded too far dissociated rapidly and swam about singly as before. From this it was suspected that conjugation might be due to the increasing osmotic pressure of the medium consequent upon evaporation. On this supposition a few crystals of sugar were added to a similar preparation, making the concentration very much higher than on evaporation, but this had no apparent effect on the zoospores. It was therefore concluded that conjugation was induced by an insufficiency in the quantity of fluid present, and this conclusion seemed to be confirmed when on placing two portions of a culture of zoospores, one in very scanty and the other in abundant water, the first quickly conjugated while the second

did not. The process of conjugation is not different from that common in various algae. Two zoospores of approximately equal size approach (fig. 38) and lie alongside each other (figs. 39, 40); the plasma membranes separating them disappear, and within a few minutes the nuclei, which may be seen as clear central bodies, have fused into one (fig. 41). The two pairs of cilia remain distinct, and in the cases observed by me there persists a slight groove in the anterior portion of the zygote indicating the line of fusion.

LAGERHEIM reports that both conjugated and unconjugated zoospores are able to infect the host. My own observations on this point gave no results. Repeated efforts were made to observe the process of infection, but for the most part the spores swam indifferently about the pieces of fresh ragweed which were placed on the slide with them. In some cases, indeed, the spores, both conjugated and single, settled down on such pieces of the host and became fastened to them with one or more cilia, but in no case did penetration occur.

My attempts at reinfection on the living plant were similarly unsatisfactory. Out of numerous attempts, only three successful infections were secured. In these cases the development of the young parasites was very rapid, but as the successful experiments were my first attempts in that direction, and as all efforts to repeat them failed, I do not feel warranted in reporting them in detail.

One of the interesting questions which the failure of the infection experiments left unsolved is how the character of the young cysts is determined, that is, whether they are to develop into resting spores or into zoosporangia. Although this is connected with the seasonal cycle in North Carolina, there is no indication in LAGERHEIM's account that such is the case in Ecuador. By analogy with other forms, one might suspect that the zoosporangia spring from unconjugated zoospores and the resting spores from zoozygospores. But there is no definite alternation of generations, as in some such forms. In any case, the character of the cyst appears to be determined immediately on infection. As may be seen from the figures, the methods of penetration and growth are different from the very beginning, so that in the very youngest cysts there is no question whatever which are zoosporangia and which are resting spores.

In very few cases was there any ambiguity in this respect, although several malformed zoosporangia were seen. In one of these a heavy wall had formed across the neck, leaving only a small pore between the neck and the body of the cyst. Several very narrow-necked zoosporangia were also observed, but though these resembled the resting cysts in shape, they were apparently otherwise normal.

MICROCHEMICAL REACTIONS.—The two outer walls of the resting spores are cellulose, as reported by LAGERHEIM, who used chlor-zinc-iodide as a test reagent. With iodine and sulphuric acid also they give the cellulose reaction, but were not in my tests as deep a blue as the cotton fibers which were used as a check. But the endospore is different in character and was unaffected by any of the reagents or stains employed.

LAGERHEIM suspected that there might be chlorophyll in some stage of the life cycle, though he was not able to detect it. The plant has more or less red pigment at all stages, but none of my observations gave any ground for supposing chlorophyll to be present.

The red pigment, as reported by LAGERHEIM, is haematochrome or some closely related lipochrome. It is colored green with iodine in potassium iodide, blue with sulphuric and nitric acids, fading away after treatment with the latter. Tests with red individuals of *Sphaerella* under the same cover-glass with *Rhodochytrium* gave somewhat contradictory results, but showed some differences between the pigments of the two. The haematochrome of *Sphaerella* was not dissolved by carbon disulphide, which is a solvent for the allied pigment carotin, even after prolonged treatment, but the pigment of *Rhodochytrium* was easily dissolved under the same conditions. The haematochrome reacted to a weak solution of iodine such as is used for testing starch, but the pigment of *Rhodochytrium* remained unchanged until a strong solution of iodine was applied, when the characteristic reaction appeared. With sulphuric acid also *Sphaerella* reacted instantly, but drops of the red oil of *Rhodochytrium* remained unchanged for several minutes and slowly turned blue. While still inclosed in the unbroken spore, the pigment is very resistant to almost all reagents. This was first noticed on fixing with chromacetic acid, which fades out

almost everything put into it. Nor did the color fade during the prolonged soaking in alcohol and hot chloroform incident to imbedding in paraffine. But when after sectioning it was treated with turpentine, it quickly dissolved. Although easily soluble in carbon disulphide after the spores are broken open, as stated above, it resists that reagent indefinitely (three months) when bits of the host plant containing the spores are treated with it. It was likewise unaffected by three months' treatment with xylol, benzene, chloroform, absolute alcohol, ether, and turpentine. It was also undimmed in brilliance after 6 days' maceration in 10 per cent hydrofluoric acid.

One of the most conspicuous features of the material was the great difference in certain respects between that collected in 1908 and that in 1910. In the former the zoospores (figs. 32–34), and for the most part the zoosporangia also, after the first division (fig. 27) were entirely destitute of starch, their cytoplasm being clear and finely granular. But in the latter the zoosporangia (figs. 15, 27) and almost all of the zoospores as well (fig. 35) were abundantly supplied with starch, which on account of its refractive and staining properties greatly interfered with the observation of nuclear phenomena. The condition of the zoospores was of course reflected in the young cysts, which in 1908 had at first clear granular cytoplasm without a sign of starch grains or any other structures (figs. 2, 3, 14), while in 1910 the cytoplasm was packed with small starch grains from the first (figs. 1, 11, 12). There were also some differences in the nuclear behavior in the two cases. Those figures which are interpreted as amitosis are almost entirely confined to the 1908 material. The plugs of the zoosporangia are also very different in the material of the two years as described below (p. 136). Moreover, there is reason to believe that similar variations occur in the Ecuadorean form, because there are discrepancies between Lagerheim's account and that portion of his material which I have examined, which would be inexplicable to me if I knew only the 1908 material of the form on *Ambrosia*. These differences serve to emphasize the caution we must use in interpreting cytological results. They can hardly fail to suggest that some of the numerous instances where one investigator does not

find what another has reported in a given species, may be due to variations in the conditions of the environment at the time of collection, the effects of which are almost entirely unknown at the present time. From the very character of the work, such errors are peculiarly liable in cytological investigations, for it is manifestly impossible within reasonable limits of time to examine thoroughly material taken under various conditions of growth over a series of years.

The question of species

On account of the great distances separating the three known habitats of *Rhodochytrium* and the diversity of its hosts, one is led to suspect that there are three species rather than one. With the idea of separating them if possible, a study was made of LAGERHEIM's and of BARTHOLOMEW's collections. Previous comparison of the North Carolina material with LAGERHEIM's description had disclosed some minor differences, but these disappeared on examination of the plant itself. In the form on *Asclepias*, likewise, I am entirely unable to detect any constant or significant differences. The various figures presented herewith show how difficult it is to find characters in *Rhodochytrium*. In size and shape there is every possible variation, and there is a total absence of such peculiarities as markings on the spores, etc., which in many groups supply useful specific characters.

It was thought for a time that the shape and size of the plugs which close the mouths of the zoosporangia were different in the three forms. LAGERHEIM describes the original *R. spilanthidis* as having a bell-shaped plug (cf. fig. 21) which did not develop until the sporangium had reached a considerable size. In the form on *Ambrosia* the plug is generally 25–35 μ long, solid, and develops early (fig. 14). The form on *Asclepias* has a similar plug, but it is usually larger, reaching a length of 60 μ (fig. 16). The condition of all the plugs in the 1908 material was fairly constant, but the 1910 material showed such variation that it became evident that the characters of the plug were worthless. Its size varies with that of the sporangium. In large sporangia on the stem it sometimes reaches 50 μ in length, and in small ones on the leaves it is

sometimes as small as 12 μ. Moreover, it is sometimes very tardy in its development. The variation in shape is likewise great (figs. 15, 17, 18, 20, 21, 24). LAGERHEIM's material shows for the most part the same sort of solid plugs. The form shown in fig. 19 was observed but twice, while bell-shaped plugs such as he figures were entirely absent from that portion of his material which I examined. It seems safe to assume that the apparent discrepancy is to be explained by the same sort of variation as that just noted in the form on *Ambrosia*.

There seems, therefore, to be no course open but to conclude that there is no morphological basis for separating the three forms. There is, on the other hand, reason to expect that they would be found to be physiologically differentiated in respect to their hosts if a series of experiments in cross infection were undertaken with one or all of the forms. Until the experimenter acquires more skill, however; than is possessed by the writer in transferring the infection from plant to plant, the expected negative results of cross-infection would prove nothing.

The range of the plant seems to call for some comment, but the data are hardly sufficient to decide whether the three known localities represent points in a single extensive range, or whether they are isolated stations. If they represent the continuous range of a single species, the limitation to such unrelated hosts raises some considerable difficulties concerning their distribution. Two of the hosts, *Spilanthes lundi* and *Asclepias pumila*, are somewhat localized species, and their range in neither case extends to either of the other stations; but *Ambrosia artemisiifolia* is widespread, and occurs both in Kansas and throughout South America. If the three forms are not physiologically distinct, therefore, cross-infection should occur naturally in Ecuador.

It seems, therefore, that the answer to the question of the number of species of *Rhodochytrium* will depend on the point of view of the student. He to whom geographical and physiological isolation are criteria of species may well conclude that there are three species, while he who demands morphological characters by which to distinguish species will decide that there is but one. Each of these points of view has its advantages, and it is not for

the writer to determine which shall be adopted by his readers. In some groups, as in the bacteria, species are perforce determined almost exclusively by physiological characters, while in other groups, as in the seed plants, morphology alone determines the matter. In the parasitic fungi various infection experiments have shown that numerous species which occur on several hosts may be composed of physiological races, each confined to its particular host. Such a treatment seems to the writer an entirely satisfactory manner of expressing the facts, and he does not see that there would be any gain in considering the forms specifically distinct.

The development of the resting spores

Although the resting spores do not appear in numbers until several generations of zoosporangia have matured and discharged, it will be more convenient to describe them before the more complex development of the zoosporangia is taken up. The very youngest resting spores seen measure about 70 μ in length (fig. 1). They consist of an elongated germ tube with an external button marking the position and size of the zoospore from which they originated. The distal end has already begun to enlarge, but the nuclei (5 μ) are not much larger than those of the zoospores. The germ tubes do not seek out the stomata even when close beside them (fig. 11), but force their way between the epidermal cells at any point. After penetrating a variable distance, usually until a vascular bundle has been reached, the tube begins to swell up and gradually it acquires a globular form. The swelling out of the cyst is very much more rapid than the growth of the protoplast, which in consequence becomes highly vacuolate (fig. 2), like an old cell far back from the growing point in an ordinary plant. There is an attenuate peripheral layer of cytoplasm connected by radial strands with the central body surrounding the nucleus, which likewise has grown but little. At the very beginning of the enlargement of the basal portion, the protoplast withdraws from the narrow neck of the germ tube, which is later cut off by a wall.

Even when full sized, the parasite distorts the tissues of the host but very little. Most of the cells which lie adjacent to it appear as though cut off to make room for its growth rather than crowded

aside by gradual pressure (fig. 15). Generally the walls of these cells can be readily distinguished from that of the cyst, though they may be closely appressed to it. Such walls usually correspond approximately in length with the adjacent part of the parasite. This indicates, especially in those cells that have been much reduced in size, that they have shrunken considerably, for the original wall would have been much crumpled if merely pushed back by the expanding parasite. They often lose their sharp outlines and appear to be undergoing digestion.

The supply of nutriment which makes possible the growth of the parasite is drawn from an extensive system of haustorial rhizoids, which are put out from the basal portion of the young parasite even before the germ tube begins to swell out into the spherical cyst. They continue to increase and to extend their ramifications until the cyst reaches its full size and begins to ripen, finally extending considerable distances along the vascular bundles. But notwithstanding the wide extension of these elements and their filamentous form, they can hardly be compared with the hyphae of a true fungus. They are by no means to be looked upon as the vegetative portion of the plant from which the fruiting bodies take their origin, but merely as rhizoidal outgrowths from the main body of the parasite. When old they develop thick walls, especially in the portions close to the cyst. But at the extremities, where most of the absorption may be supposed to occur, the wall is exceedingly delicate or invisible. Although they sometimes work their way between the disorganizing cells, their course is for the most part within the cells which they invade (fig. 5), and their shape is often largely determined by the boundaries of these cells. Both LAGERHEIM and ATKINSON speak only of those haustorial branches which become attached to the vessels of the system. But the great mass of the rhizoidal system is located in the phloem (figs. 4, 5, 15, 22), and it is the cells of the phloem which are most injured, finally breaking down completely, while the xylem is but little injured. It must also be obvious that the vessels could not furnish the supply of organic food necessary to nourish the parasite. There is no doubt, however, but that some of the ultimate branches of the haustoria do come into close relation

with the vessels, exactly as described by LAGERHEIM and ATKINSON (fig. 5), and probably draw water from them. These terminal haustoria (fig. 6) are closely appressed to the thin places between the spiral thickenings of the vessels, but appear not to penetrate them as in the phloem.

With the development of the rhizoids the protoplasmic contents of the cysts become more abundant and denser. The nucleus increases in size and undergoes a metamorphosis like that of the zoosporangium described below. Starch grains, if not already present, appear and become large and abundant, until they pack the cyst so full that its cytoplasmic contents proper may become almost invisible. In this process all vacuoles disappear and apparently all surplus water is eliminated. Even the aqueous karyolymph partially disappears, causing the nucleus to collapse (figs. 7, 8). In this condition the nucleus differs so far from ordinary healthy nuclei that it is difficult to believe that this change is not pathological. But it seems to be a universal and perfectly normal phenomenon. On the beginning of germination in the spring, the nuclei again become turgid, though they are apparently smaller than before shriveling up.

When the vegetative activity of the parasite is ended, as indicated by the shriveling of the nucleus and the withdrawal of all of the starch from the rhizoids into the spore, a second cellulose wall is laid down on the inside of the spore (fig. 7) and sometimes in the proximal ends of the rhizoids as well (fig. 5). But either at the time of deposition of the second layer of the spore wall or soon afterward, the rhizoids are cut off from the spore first by a plasma membrane and later by a definite wall. This is soon followed by the disorganization of the contents of the rhizoids. The second wall of the spore is quickly followed by the formation of a third (fig. 8), a thick, non-cellulose endospore, which completes the preparation of the spore for its period of rest.

The starch grains

One of the most interesting things about *Rhodochytrium* is the fact that though it is a parasite and has completely lost its chlorophyll, it forms starch in considerable quantities. The source of

this starch is of course the photosynthetic activity of the host, but it is hardly necessary to state that the starch grains of *Rhodochytrium* are quite different in form from those of the adjacent host cells.

As would be expected, starch is most abundant and best developed in the mature resting spores, in which it forms the bulk of the reserve food, but it may be present at any stage in the life cycle. In the zoosporangia it is nearly always present toward the end of the vegetative period, but there is a decided tendency to consume it during the period of nuclear division. A marked difference was noted in respect to starch content between zoosporangia gathered in 1910 and those gathered in 1908. In the former both zoospores and very young sporangia contain numerous starch grains, but in the latter starch appears tardily and almost always disappears before segmentation, leaving the cytoplasm clear and granular, without inclusions of any sort.

The grains seldom exceed 10 μ in diameter and are commonly somewhat smaller. They are usually spherical or somewhat elongated, but very long or double grains are not rare (fig. 9). The larger grains when mounted in balsam frequently show conspicuous cracks at the hilum, as is not unusual in starch grains generally. No definite alternating concentric layers of different refractive indices such as characterize many starch grains could be made out, but in certain grains faint concentric striae appeared to be present. When subjected to the action of strong chromic acid, they show during dissolution the radial structure characteristic of starch grains in general.

STARCH GRAINS UNDER POLARIZED LIGHT.—In the dark field obtained by crossing Nicol prisms, the starch grains show the usual luminous body crossed by dark bars in the two planes of polarization (fig. 10). But there is considerable variation in the behavior of different grains, both in those of the same cyst and in different cysts taken as a whole. Almost all conditions, however, may usually be found in a single cyst. Many of the spherical grains show no change other than the revolution of the crosses when the prisms are rotated, demonstrating in these grains a perfectly symmetrical structure, with the hilum occupying a point in the

center. In elongated grains the crosses resemble those in leguminous starch, namely, a pair of Ys arranged bottom to bottom, indicating an elongated hilum. And in double grains, which are not infrequent, the stems of the Ys are sometimes divided, so that the very center of the grain appears bright. Such grains are of course unsymmetrical, and show the characteristic crosses only when the planes of polarization form the proper angle with the axes of the grain. There are also great differences in the brilliance of the grains; some are very beautiful objects, but others repolarize the light to such a slight extent that they are very faint and the dark crosses are difficult to see. Frequently, indeed, the grains become entirely black and vanish completely when the prisms are crossed. When this happened, I was inclined to suspect that I might have mistaken grains of some other substance for starch, but on running iodine under the cover the characteristic blue reaction promptly appeared to dispel all such doubts.

ABSENCE OF PLASTIDS.—It is unsafe to assert, perhaps, that there are no plastids in *Rhodochytrium*, but it is certain that methods which bring them out clearly in such objects as old potato tubers failed to reveal them in *Rhodochytrium*. So far as could be determined, the starch grains are formed directly in the cytoplasm without the intervention of plastids, pyrenoids, or other specialized protoplasmic bodies. There was only one feature which could be taken to give any indication of such bodies. Many of the grains do not stain uniformly throughout, but show a more deeply colored margin. This appearance is not confined to grains of any particular size, but is found from the smallest to the largest grains. Indeed, when present at all the border is usually wider and more conspicuous in the large grains than in the small. It occurs rather on certain slides or perhaps on certain pieces of material, being present in nearly all of the cysts of some slides while absent from others. The border appears to have the same crystalline structure as the rest of the grain, and seems definitely to be a part of it rather than a separate surrounding body. In no case did it present the granular appearance to be expected of a plastid. I have no satisfactory explanation to offer for this phenomenon, but I do not believe it is permissible to interpret it as a plastid.

Almost ideal conditions for observation of the process of starch formation are sometimes presented in very young zoosporangia (fig. 11), where the cysts are highly vacuolate, with delicate strands of cytoplasm stretched from side to side. In thin sections such strands are suspended across the cyst, with no adjacent objects to interfere with vision. Frequently these strands show all stages in starch formation (fig. 11*a*) from good sized grains down. The larger grains are clear cut, sharply outlined against the clear cytoplasm in which they are suspended. From such well-formed grains there is an unbroken series of smaller and smaller grains down to the limit of visibility. The very earliest stages appear as mere knots in the cytoplasm, while the definite characters of starch grains appear as soon as the body reaches a size large enough to be resolvable into an area rather than a point. At no stage was anything seen in association with the starch grains except morphologically undifferentiated cytoplasm. More often, of course, the grains are formed in large masses of cytoplasm where the opportunities of vision are not so good, but here also they appear to lie naked in the cytoplasm.

The classic examples of the formation of starch grains without differentiated plastids were described by STRASBURGER (26, pp. 155 ff.). He found that in the megaspores of *Marsilea* and in the medullary rays of *Pinus* the growing grain was invested by numerous microsomes, which he believed secreted the starch in a manner analogous to the formation of the cell wall by the granules of the spindle fibers at the close of mitosis. These microsomes were large enough to appear as definite granules under a comparatively slight magnification (450 diameters). In *Rhodochytrium*, however, no such microsomes could be made out under a magnification seven times as great.

It should be added also that in those stages where starch is absent the cytoplasm is smooth and granular, without inclusions of any sort. If perchance the writer had overlooked the plastids among the grains during starch formation, he would have expected to see them here, if present. If there are any plastids, therefore, they would appear to be formed *de novo* rather than carried over from generation to generation as permanent organs of the cell.

The development of the zoosporangia

As already stated, the zoosporangia are distinct from the resting spores from the very beginning. The youngest stages seen were approximately as large as the youngest resting cysts, namely, 60–80 μ in length. These future zoosporangia do not form external buttons, and the neck, even at the very first, is of comparatively large diameter (fig. 12). While still very young, the cyst begins to swell out from the initial tubular form, and soon assumes the roughly turbinate shape characteristic of the mature zoosporangium. But before the parasite begins to expand, it generally penetrates straight into the tissues until it has reached the vicinity of a vascular bundle. The final size of the cyst is roughly proportional to the length attained by the germ tube, but of course the relation is somewhat accidental, since it is the stronger bundles capable of supplying more abundant food which are the more deeply buried. In the leaves the distance is approximately 100 μ, while in the stems, where the vascular bundles are relatively deeply buried beneath the cortex, a length of 300 μ or more is frequently attained (fig. 14). It thus happens that size is no criterion of the age of a cyst, some uninucleate cysts being much larger than some which are far along in division, as shown by figs. 12 and 26, which are drawn to the same scale.

Sometimes, while still in the tubular condition and usually before full size has been reached, a characteristic plug is formed at the mouth of the zoosporangium. In all but the youngest stages this is the most convenient character for distinguishing the zoosporangia from the resting spores, since the latter never develop a plug. But the plug is subject to great variations in size, and in rare instances may never develop at all. The most typical form is a solid top-shaped mass which stains deeply and uniformly throughout (figs. 14, 15, etc.). Often it is a hollow, bell-shaped structure (fig. 21), as figured by LAGERHEIM (see above, p. 136). In some instances such bell-shaped plugs were found to be perforated so as to place the interior of the cyst in open communication with the outside. Some solid plugs were observed which stained lightly, except on the lateral edges (fig. 24), giving the appearance of bell-shaped plugs which had been later filled up. In many cases the

plug is secondarily surrounded by several concentric layers of material, evidently laid down at intervals. Such plugs show great variation in appearance (figs. 17–20), presumably on account of variations in the conditions of deposition.

As in the resting spore, the protoplast is at first highly vacuolate, consisting of a peripheral layer of cytoplasm connected with the central mass about the nucleus by radiating strands. As growth proceeds, the cytoplasm becomes more abundant in proportion to the vacuoles, but the zoosporangia always have larger vacuoles than the resting spores. Sporangia of different ages, however, vary considerably in this regard. The larger cysts usually have larger vacuoles than the smaller. In later stages there is always one large vacuole which occupies the upper half of the cyst, the protoplasmic contents, except for a thin peripheral layer, being confined to the basal portion, as shown in the figures. The numerous rhizoids which are put out from the base are like those of the resting spore.

The cysts reach full size before there is any indication of division. But when division commences, the binucleate, tetranucleate, and later stages follow each other in rapid succession (figs. 22–28), until a large but variable number of nuclei have been formed. Upon completion of the period of nuclear division, segmentation occurs and zoospores are produced. The coenocytic cysts are comparatively rare. Never, even in the most favorable material, do they approach in abundance the primary cysts or those in which segmentation is complete.

The shape of the cysts seems to be determined largely by accidental variations in the compactness
lie. The penetrating germ tubes foll
of least resistance. This sometimes
the tissues (fig. 2), and causes conside
of the mature cyst.

In those cysts which have abundan
corresponding in size and shape witl
for some time after division (figs. 2
are found sometimes in the telophases
These are not vacuoles, as might a

with the starch-filled cytoplasm surrounding them, but are occupied by cytoplasm similar to that of the remainder of the cyst, except that it is free from starch. This condition endures for a variable period; it sometimes disappears during the binucleate stage (cf. fig. 23), and sometimes persists into the octinucleate stage (fig. 24).

The nuclei of the early stages of the coenocyte tend to remain in the central position originally occupied by the primary nucleus, but later scatter, finally becoming evenly distributed through the cytoplasm. The period at which they disperse varies, as would be expected. One case was found in which they were still closely bunched in the 16-nucleate stage (fig. 25), but they are usually dispersed a little before that time.

SEGMENTATION.—On account of certain apparently conflicting processes observed, the writer has not been able to satisfy himself altogether concerning the mechanism by which the coenocytic cyst is cut up into spores. The account here given is therefore somewhat tentative.

During the last mitoses in the sporangium, a change seems to come over the protoplasm of the coenocyte. Up to this time the nuclei have apparently lain freely in the common cytoplasm without any tendency to form separate cells. But during these mitoses the cytoplasm appears to contract around the spindles and to draw up closer to them, so as to leave vacuoles in the intermediate spaces (fig. 30). These vacuoles, surrounding, as they do, the separated masses, often resemble cleavage furrows cutting the coenocyte up into individual cells. The cytoplasmic edges of the segments do not present the sharp clean outlines seen in progressive cleavage, however, but appear more or less irregularly frayed, and frequently cytoplasmic strands cross the vacuoles and connect adjacent masses.

These connections would seem to put aside any interpretation of the process as due to cleavage furrows, but one cyst was observed in which the margins of the individual masses were clear and sharp, without any bridges across the furrows (fig. 29). This case was difficult to interpret otherwise than as progressive segmentation by cleavage furrows.

This cytoplasmic contraction appears to be a universal occurrence, having been seen in all of the numerous cysts of this age observed. Nevertheless, in the writer's judgment it is not to be interpreted as segmentation. That appears to be a distinct process of a different nature. Since the preliminary contraction occurs during mitosis, it gives rise not to uninucleate but to binucleate segments. No indication of a constriction separating the daughter nuclei was seen in the telophases observed (figs. 63–65). The steps connecting this condition with what I take to be true segmentation could not be made out, but it would seem probable that the contraction disappears after mitosis is complete and the protoplasm of the cyst again becomes a continuous coenocyte. It will be understood that a regressive change of this character would be difficult to demonstrate except in living material, which in *Rhodochytrium* is too thick and too deeply pigmented to permit the observation of details of this sort. If the zoospores were always the same size, or if segmentation always occurred after a given number of nuclear divisions, it might be possible to recognize those cysts which had passed through their last mitosis and were ready for the final segmentation, but both the size of the zoospores and the number formed in different sporangia vary to such an extent as to make it impossible to distinguish those sporangia which have completed the cycle of mitosis from those which have not.

But whether the cysts again become continuous coenocytes or not, there is another sort of cleavage, which I take to be true segmentation, that appears to delimit the spores without reference to the separations brought about during the preliminary contraction. This occurs by the precipitation of membranes around the protoplasmic units (fig. 31). Each nucleus with its quota of cytoplasm is cut off from the rest by a membrane which appears within the strands of cytoplasm after the fashion of free cell formation in the endosperm of a seed plant. The membranes of the protospores are very delicate, but the method of their formation seems to be clearly indicated in the preparations. If one observes a protospore which is not yet completely surrounded, the terminal portion of the advancing membrane will appear simply as a heavy

strand of cytoplasm (fig. 31, *a*). The spores seem to round off soon after their membranes are laid down, presenting as they do so somewhat the appearance of bodies being divided by advancing cleavage furrows. Observation of the terminal portions of the apparent furrows shows, however, that they merely separate spore membranes already formed by precipitation within the cytoplasm. This is made especially clear at the angles of the protospores, where the membranes frequently cut across the corners, leaving small portions of the cytoplasm which do not enter into the formation of any spore (fig. 31, *b*).

Maturation of zoospores.—Although the protospores quickly round off and separate from each other, they remain in the position occupied before segmentation. Consequently the mass of young spores retains the shape of the coenocyte from which it was derived, leaving the central vacuole unoccupied as before segmentation, as in fig. 28, which shows the condition of the great majority of the segmented cysts observed. In such sporangia the young spores are usually regular ovoid cells (fig. 33), without the differentiation of parts characteristic of the mature spore. Only rarely were fully matured zoospores which had moved out into the cavity of the cyst found in the sections studied. In such ripened spores there is a conspicuous differentiation into anterior and posterior ends (figs. 35, 36). In the posterior end is collected the larger part of the cytoplasm with the starch grains, if any be present, while the anterior end appears highly vacuolate in fixed preparations on account of the removal of the pigment which occupied it during life.

In no case was I able to assure myself that cilia were present in the section studied, although I thought I saw them several times. This was probably due to imperfect fixation, since the chromacetic acid used is not as well adapted for preserving such structures as some killing fluids which might have been used had it been possible to experiment on the ground. In zoospores fixed in osmic fumes, after liberation the cilia were of course clearly shown (fig. 37), and in these, as well as in many of those on the sections (fig. 36), there was a conspicuous deeply staining body at the base of the cilia such as has been found in zoospores of many other forms. In many of the spores, especially those a little over-

stained, one or sometimes two delicate connections could be seen between this basal body and the nucleus (fig. 34). The origin of the basal body was not made out. Apparently it appears only during the maturation of the spore, for it was not observed in earlier stages (figs. 32, 33).

The primary nucleus

Although the youngest cysts observed are many times larger than the zoospores from which they originated, their nuclei show comparatively little enlargement. But they differ somewhat in character from the nuclei of the zoospores in that the concentration of the chromatin, which, as shown above (figs. 32–37), begins in the maturing zoospore, has been completed, forming the karyosome, which is the most conspicuous element of the nucleus. But the karyosomes of the young cyst have not acquired the character of the later nucleoli. From the irregularity of their shape they appear to be merely plastic masses of chromatin (fig. 42). They soon take on the definite spherical form of mature nucleoli, and at the same time probably become firmer, inasmuch as in the later vacuolate stages the rind is strong enough to retain its shape after most of the contents have been withdrawn. The linin reticulum seen in the sporangial segments probably persists on the periphery of the nucleus in the youngest stages, but it loses its affinity for stains and is exceedingly difficult to see satisfactorily. All that can be made out with certainty in most of the nuclei is a few delicate linin strands stretching from the karyosome to the nuclear membrane (figs. 1, 13), or, in optical section, a number of peripheral granules (figs. 2, 12), which probably represent cross-sections of the similar strands that compose the reticulum, but are too faintly stained to be visible in surface view.

No differences between the nuclei of the incipient zoosporangia and of resting spores were detected. From the youngest stages on they undergo the same development, which in one case leads to mitosis and in the other to shriveling preparatory to the long dormant period.

The most conspicuous of the changes in the nucleus is its increase in size. From 4 or 5 μ it grows with the cyst until it may reach

the enormous size of 50–60 μ (figs. 15, 45). This size, however, is attained only in the largest zoosporangia. The nuclei of the resting spores are never so large as those of the zoosporangia, which themselves vary greatly, being roughly proportional to the cysts in which they occur. In extremely small cysts the nucleus may never exceed 15 μ, though few are smaller than 20 μ at maturity. In the largest nuclei the increase in volume during growth is almost 10,000 fold. There are but few organisms in which any single nucleus grows to such an extent without division, but *Rhodochytrium* is by no means unique in this respect. In *Synchytrium*, by reason of the minuteness of the zoospores, the increase is very much greater, amounting sometimes to 50,000 fold. In some of the cycads, especially *Dioon* (CHAMBERLAIN 5), the increase in volume must be nearly as great, since the mature nuclei reach 500–600 μ in diameter. The nuclei of some animal eggs, for example *Dytiscus* (DEBAISIEUX 7), also show great increase in volume, but not so much as in the plants just cited.

For the study of the vacuolation of the nucleolus, *Rhodochytrium* and *Synchytrium* probably afford better opportunities than any other organisms, although an analogous process occurs in many plants. Occasionally in *Rhodochytrium* a single central vacuole appears to increase in size until only a thin rind of stainable substance remains. In other cases the whole nucleolus becomes honeycombed with numerous small vacuoles (fig. 46), which later coalesce (fig. 47) into a large central cavity (fig. 44), which continues to increase in size until finally the old nucleolus, originally a karyosome, becomes a plasmosome, collapses (fig. 45), disintegrates, and finally disperses in the cytoplasm during mitosis.

Intimately connected with the history of the nucleolus, and in many ways perhaps even more interesting, is the behavior of the chromatin. As may be seen from figs. 2, 12, 42, the whole of the chromatin is at first concentrated in the karyosome, and from it all of the chromatin of the primary nucleus is derived. While the nucleus is still comparatively small, vacuoles begin to appear in the center of the karyosome (figs. 3, 13, 14), and the characteristic irregular masses of chromatin begin to fill the nuclear cavity. As

in *Synchytrium*, these are most abundant in the vicinity of the nucleolus (karyosome), frequently touching it. Closer examination will often reveal many in the act of budding out from it (figs. 43, 47). During the growth of the nucleus there is, of course, an enormous increase in the amount of chromatin it contains. This increase of the chromatin probably takes place both in the nucleolus during its growth and in the free chromatin of the nuclear cavity. But the withdrawal of the chromatin from the nucleolus must be more rapid than its formation therein, since the vacuolation of the nucleolus increases with age. The linin reticulum, which, as has been seen, loses its affinity for stains in the young cysts, never reappears in the primary nuclei. The chromatin, as it is withdrawn from the karyosome, does not seek the nuclear membrane, but is distributed through the nuclear cavity. In the early stages of growth the chromatin spherules are often connected by indefinite strands of linin, which anastomose to some extent through the nuclear cavity (figs. 3, 14, 44). But in many of the nuclei (fig. 43) such linin connections never appear, and in any case they disappear before the nucleus reaches its full size. In mature nuclei (fig. 45) the chromatin appears as amorphous, almost flocculent, spheroidal masses scattered through the nuclear cavity, singly or in loose chains. The amount of chromatin and the size of its masses vary considerably in different nuclei. In some cases there are relatively few large globules, while in others the chromatin, in a comparatively fine state of division, almost fills the cavity of the nucleus. The small intensely staining granules, which are so conspicuous against the membranes of the primary nuclei of *Synchytrium*, are seldom observed in *Rhodochytrium*, but in some instances (fig. 57) were as prominent as in *Synchytrium*.

The peculiarities of the primary nucleus characterize to a large extent the nuclei of the binucleate and tetranucleate stages, but gradually disappear as the nuclei become smaller, until, from about the 32-nucleate stage on, the nuclei resemble those commonly found in other organisms. Except in the very latest stages, however, both the chromatin granules and the linin connections are coarser than in most nuclei.

Mitosis

There are two types of mitosis in *Rhodochytrium*. The first type occurs in the earlier divisions of the zoosporangium, while the second is found in the last divisions before sporulation. They are not, however, to be considered as distinct, for they merge into each other.

No evidence of a reduction division was found. Nowhere were nuclei seen in fours, as would be expected after reduction; and while the chromosomes are difficult to count accurately, I feel sure that their number was approximately the same in the last divisions as in the primary mitosis. They are extremely difficult to count, however, because they are usually close together and often surrounded by starch grains. For this reason it was not possible to count the chromosomes of as many spindles as would have been desirable, nor to insure exactness in the cases counted. In all of the cases where counting was attempted, however, the number was no smaller than 8 nor larger than 10.

The assembling of a series of stages of mitosis is an exceedingly tedious task. As already stated, coenocytic cysts of any sort are comparatively rare. Those in mitosis are of course rarer still. It is doubtful if one cyst in a thousand of those observed showed dividing nuclei. The anaphases and telophases are particularly difficult to find. It was not possible, therefore, to examine a large number of figures of the different stages. But inasmuch as the spindles found form a concordant series, it is believed that the account given accurately describes the process.

MITOSIS OF THE FIRST TYPE.—The typical mitosis of the first type is the division of the primary nucleus, but the second and third mitoses are so similar that for purposes of description they may be said to be identical. Drawings from all of these have been used in the plates indiscriminately, but they may be identified, if desired, by the explanation of the plates.

Spindle formation.—The first indication of approaching mitosis consists in the appearance of kinoplasmic fibers among the masses of chromatin in the nucleus. The change shown in fig. 48 is so slight that it would hardly have been detected had not the other nuclei of the cyst been already far advanced in spindle formation,

thereby drawing attention to the laggard. Coincident with the appearance of these kinoplasmic fibers the chains of chromatin usually break up, and the individual masses become more definitely spherical, karyosome-like structures. In a nucleus a little further advanced the fibers have become more abundant and permeate all parts of the nuclear cavity (fig. 49), and on some of them are seen small deeply staining granules whose origin, fate, and function are not altogether clear to me.

From the very first the position of one of the poles of the future spindle can be recognized in the focus of certain of the fibers (figs. 48–50). Curiously enough, however, the other pole does not seem to appear until somewhat later, so that the young spindles show a considerable difference in the two poles, one being more fully formed than the other (fig. 51). This is such a peculiar phenomenon that one is strongly inclined to believe, when he finds such a nucleus, that he has overlooked the opposite pole on another section (most of the spindles are of course somewhat oblique), but careful search almost invariably failed to reveal it. Fig. 50, which is a sagittal section of a primary nucleus, shows perhaps the extreme of this condition; notwithstanding the strong development of kinoplasmic fibers in the part of the nucleus drawn, they were entirely absent from the other parts. It is quite possible that the spindles seen in these stages were unusual, but the occurrence of the unipolar condition in different pieces of material killed in different years has convinced me, against my prejudices, that this is a normal and usual method of spindle formation.

Such a drawing as fig. 50 resembles the prophase in the Ascomycetes, in which the linin strands containing the chromatin radiate from one side of the nucleus. There are, however, important differences between the two. The polarity of the ascomycetous spindle is determined by the presence of centrosomes attached to the nuclear membrane, but in *Rhodochytrium* no centrosomes are visible, and the pole does not necessarily touch the nuclear membrane at all. The origin of the bipolar condition is entirely dissimilar. In the Ascomycetes the two centrosomes, derived from the fission of one, separate and migrate to opposite sides of the nucleus, each carrying with it its quota of fibers with attached

chromatin. But in *Rhodochytrium* the second pole is formed, like the first, by the convergence of certain fibers to a point. In nuclei a little older than that shown in fig. 50, some of the kinoplasmic fibers can be seen to intersect at points more or less directly opposite the first pole. There are usually two or three such points (fig. 51), from each of which a few fibers radiate. In later stages one of these focal points becomes more prominent than the others, until ultimately it becomes the second pole of the spindle, as prominent and definite as the first.

In the fully formed spindle the larger proportion of the fibers of course stretch from pole to pole, but in the early stages the rays from each pole appear as an independent fascicle radiating from the focus, with little regard to the position of the opposite pole. The vestiges of this condition may be seen in fully formed spindles, in which many of the acicular mantle fibers stretch straight by the equator of the spindle, intersecting those from the opposite pole (figs. 52–54). Not infrequently a few fibers center in the pole and do not enter into the formation of the spindle, but radiate into the nuclear cavity. In one instance such radiations were so numerous as to give the appearance of a conspicuous aster (fig. 53). But comparison with the opposite pole shows that the effect here produced is largely accidental. Nothing similar was seen elsewhere.

Chromosome formation.—The differentiation of the chromosomes, in my material, is a much more difficult matter to follow than the formation of the spindle. Of the masses of chromatin which are distributed throughout the nuclear cavity, part remain free and part become connected with the developing spindle fibers. In addition to these, some of the spindle fibers, especially in the early stages, are studded with smaller chromatic granules whose significance, as stated above, is obscure to me. At one stage of the investigation I was inclined to believe that these were used in the formation of the chromosomes, but further observation has led me to the conclusion that it is the large chromatin masses which give rise to the chromosomes. Whether the chromosomes are derived exclusively from the latter is not certain, but such figures as no. 51 show at least that some of them are utilized in chromosome formation.

The formation of the chromosomes, though it presents certain striking peculiarities, conforms in its essential features to the process usually found in dividing nuclei in other organisms. As is not unusual, spindle formation and chromosome formation, being in a sense unconnected processes, may go on side by side with a certain degree of independence, so that in two nuclei of the same age one may have the more mature spindle, while the other has advanced further in chromosome formation (figs. 52, 53).

Spirem formation will be understood by a glance at fig. 51. Between those chromatin spherules which lie in the equatorial region of the nascent spindle there arise connecting bands of linin, forming an irregular spirem. At first the stains differentiate the chromatin and the linin elements, but in later stages the spirem stains homogeneously like other spirems. In the beginning its position may not be so definite, but as it contracts it comes to lie wholly within the spindle (fig. 52). After some further contraction it segments into chromosomes in the usual way (figs. 53, 54).

Only a small portion of the chromatin of the primary nucleus is utilized in the formation of this spirem. On the dissolution of the nuclear membrane the remainder is cast out into the cytoplasm. There is no indication of any difference between those chromatin masses which are cast out and those which enter into the spirem, nor of any principle of selection other than that occasioned by the mere position of the masses which are utilized. Sometimes the masses of discarded chromatin persist for some time as deeply staining globules in the cytoplasm (fig. 22), but more often they lose their affinity for stains before the nuclear membrane breaks down and cannot be followed in later stages.

During metaphase the spindle, which previously may have been shorter than the diameter of the nuclear cavity in which it lay (fig. 53), begins to elongate, piercing the membrane (fig. 54), and later, as the membrane weakens preparatory to dissolution, distorting the nucleus (fig. 55). The only anaphases seen were of the first type, occuring in the fourth mitosis. Apparently the chromosomes are drawn away from the equator in the usual way (fig. 56). No stages showing the formation of the membranes of the daughter nuclei were seen in spindles of the first type, but two

recently divided binucleate cysts were found. Their chromatin strands (fig. 57) still showed by their orientation the position of the chromosomes from which they had been derived. As stated above, the position of the mother nucleus is still clearly indicated by a starch-free area in the cytoplasm.

No centrosomes or asters, except the pseudoaster above noted, were seen in connection with any of the spindles. The poles are very sharp, without any surrounding zone of denser cytoplasm in which a centrosome might have been concealed. There is no indication that astral bodies have any part in the formation of the nuclear membrane, as in *Synchytrium decipiens*.[3] While but very few of the critical stages were seen, it seems evident that, if there were any such conspicuous asters as in that plant, they would certainly have appeared in the preparations studied.

In the intermediate mitoses, spindle formation conforms in a general way to that in the primary nucleus, but the metaphases (figs. 58, 59) are so different that at first sight they would seem to be of an entirely different type. The differences, however, are not so great as would appear. In the smaller nuclei nearly as great an amount of chromatin is used in the formation of the chromosomes as in the larger. Their spirems are therefore much larger proportionately, and, instead of lying within the spindle, stretch nearly across the nuclear cavity. Sometimes such spindles show a considerable amount of chromatin which is not utilized in the formation of the chromosomes, but is cast out, as in the earlier divisions. Frequently, however, all of the chromatin goes into the spirem (fig. 59). The karyosome, which is so strongly developed in the primary nuclei, becomes gradually less and less prominent in later nuclei, until in the many-nucleate cyst the chromatin assumes the condition of a typical reticulum, although it is not finely divided, but remains in rather large masses which are connected by coarse linin strands (figs. 27, 29). In consequence of the different dispositions of the chromatin in these nuclei, the residual chromatin cast out during their mitosis does not take the form of large spherules, but is finely subdivided (fig. 58). Such a condition was also seen

[3] *S. taraxaci* is without karyodermatoplasts according to the recent results of BALLY (Jahrb. Wiss. Bot. **50:** 110. 1911).

in one primary nucleus, in which case the residual chromatin was much more abundant than in the smaller nuclei.

Mitosis of the second type.—The second type of mitosis is limited to the last few divisions before sporulation. Unfortunately nearly all of the mitoses of this type that were found occurred in cysts packed full of starch, which greatly interfered with observation.

The difficulties occasioned by this cause were especially serious in studying the prophases. In the cyst from which the figures of prophase were taken, all stages of prophase were certainly present, but could not be made out satisfactorily. The nuclei of the upper half of the sporangium had already passed into the metaphase, while those in the rhizoidal end were still in the vegetative condition (fig. 60), and above them all transitions to metaphase were present. As far as could be determined, these prophases were similar to those of the smaller nuclei of *Synchytrium*. A spirem is formed which in this case involves but little change from the vegetative condition. This then shortens and thickens until it comes to occupy only the equatorial region of the nucleus (fig. 61). The spindle then appears, whether as a new formation or as a metamorphosis of linin strands as in *Synchytrium* could not be determined.

The chromosomes in this type of mitosis are small and spherical (fig. 62), but apparently stretch out somewhat in fission, for at the poles in telophase they are distinctly oblong (fig. 63). In early telophase they are bunched together in a compact mass resembling the familiar "daughter star," but later begin to spread out (fig. 64) and assume irregular shapes (fig. 65), while vacuoles of karyolymph begin to appear among them, soon producing the characteristic vegetative nuclei (fig. 66). As may be seen from the figures, these stages are practically similar in all respects, save in the absence of cell plate, to the familiar anaphases and telophases of the higher plants.

Amitosis

Amitosis, which forms such a conspicuous feature of the cytology of *Synchytrium*, is almost absent from the zoosporangia of *Rhodochytrium*, or at least from the material studied. The nuclei of a few

cysts, however, are in such a condition that it seems hardly possible to interpret them as sister products of mitosis. Their chromatin assumes the condition of an extremely long and complicated spirem, which winds not only around the surface of the nucleus but fills its cavity (figs. 67, 68). Their shape is extremely irregular. The largest have developed pseudopodium-like outgrowths, which appear to have been constricting off into daughter nuclei. With these large nuclei are a number of small ones, apparently the results of the process. While the mere irregularity in the outlines of these nuclei would not in itself be conclusive evidence that they were dividing amitotically, the great diversity in the sizes of adjacent nuclei would be difficult to account for on any other hypothesis. For in *Rhodochytrium*, as in coenocytes generally, the mitoses are simultaneous, and the daughter nuclei are of approximately equal sizes (figs. 22–27). It is evident that such a process could not normally give rise to irregularities in either number or size of the resultant nuclei.

There is no indication, however, that amitosis is a normal process in the zoosporangia of *Rhodochytrium* as in *Synchytrium*. It gives rather every indication of being a pathological phenomenon.

Cytological comparisons

PRIMARY NUCLEUS.—The primary nuclei of *Rhodochytrium* are certainly very peculiar; indeed, if the cytology of *Synchytrium* were not known, we should say they were unique. But when mature they are strikingly similar to those of *Synchytrium*, or at least to those of *S. decipiens* and *S. puerariae*. The conditions sometimes found during the early portion of the growth period, however, are not paralleled in *Synchytrium*. The early stages of *Synchytrium* are very similar to the mature nuclei, but in the young nuclei of *Rhodochytrium* the chromatin spherules are often suspended on anastomosing strands of linin within the nuclear cavity (figs. 3, 14, 44). This condition is evidently less removed from the typical peripheral chromatin-linin reticulum of most nuclei than are the mature nuclei or those of *Synchytrium*.

The irregular masses of chromatin in the primary nucleus of *Synchytrium* are termed by KUSANO (18) secondary nucleoli. He

shows, what I have myself observed, that they may pass through a process of vacuolation accompanied by the extrusion of chromatin analogous to that of the primary nucleolus. In *Rhodochytrium* such secondary vacuolation occurs but rarely, though some of the largest chromatin masses may break up in this way (fig. 49). But, as was shown in the account of mitosis, a large proportion of the chromatin spherules suffer the same fate as the old nucleoli, primary and secondary, of *Synchytrium*, namely dissipation in the cytoplasm. There is, moreover, a great variation in the size, composition, and behavior of the secondary nucleoli in *Synchytrium* (see KUSANO 18, p. 94), some of them (the earlier and smaller) being almost, if not entirely, pure chromatin, and undergoing but little change in preparation for mitosis; while others (the later and larger) are plasmosomes with but little chromatic material. There is, therefore, no question but that the chromatin masses of *Rhodochytrium* are homologous to secondary nucleoli, but it does not seem advisable to use that term in describing them, since there is no distinction between those which form the chromosomes of the spindle and those which perish.

MITOSIS.—The first mitoses of *Rhodochytrium* and *Synchytrium* are not so similar as are the primary nuclei, but they are of the same general type. Although very different from those found in most organisms, the first mitosis of *Rhodochytrium*, like the vegetative condition of the primary nucleus, is not so widely aberrant as that of *Synchytrium*. Neither STEVENS nor KUSANO was able to obtain an altogether satisfactory series of the prophases of the primary mitosis, and their figures do not supplement each other, but conflict to a certain extent. Both observed, however, a marked and peculiar production of fibers, STEVENS through the whole cavity of the nucleus, and KUSANO especially in the region of the old nucleolus after the dissolution of the membrane. While the conditions found by these writers in *Synchytrium* differ greatly in detail from those in *Rhodochytrium*, the fibers would seem to be comparable to those seen in the early prophases of the present plant. If this interpretation is correct, the fibrous stage in *Synchytrium* is not to be homologized with a spirem, but is rather a phase of spindle formation. The differentiation of the chromosomes,

which neither of these writers was able to observe, would on this assumption be a distinct process. While it cannot be predicted that in the differentiation of the chromosomes *Synchytrium* will be found to resemble *Rhodochytrium*, it is clear that in the formation of the spindle there is considerable analogy.

While the metaphases, and probably the prophases as well, of the second type of mitosis are similar to those of *Synchytrium*, this has no particular significance, since they present no peculiarities, but are similar to those of many other organisms. The telophases, however, differ considerably from those of *Synchytrium*, both in general form and in the absence of the conspicuous kinoplasmic asters, *karyodermatoplasts*, which in *Synchytrium decipiens* and *S. puerariae* form the nuclear membranes of the daughter nuclei. These structures remain, therefore, peculiar to these species.

KARYOLYMPH.—The large primary nuclei, of course, are cut into several sections by the microtome. The central section of such a nucleus presents an appearance which would hardly be recognized by the uninitiated, for it looks at first sight like a hole in the cytoplasm of the parasite. It is surrounded, however, by the nuclear membrane and contains some of the amorphous masses of chromatin and perhaps a part of the nucleolus. But sometimes the whole nuclear cavity is filled with a frothy mass similar to that noticed by KUSANO in *Synchytrium* after fixation with Keiser's fluid. It appears to be, what KUSANO interpreted it, a precipitation from karyolymph. I have not figured it because it is inconstant in occurrence and imperfectly understood.

It should be noticed here, however, that the karyolymph may very likely play a much more important rôle in cell physiology than is at present assigned to it by cytologists. It is dismissed with a sentence in such texts as WILSON'S *Cell*, because our knowledge of it is practically nil. Yet, ignorant as we are, a little reflection will convince us that it must be of some consequence to the cell. On the amount of karyolymph depends the size of the nucleus, for it is in reality merely a vacuole of karyolymph around which is stretched the chromatin reticulum. It is a well-known fact that by some means the size of this vacuole is maintained with slight variation in the cells of a given tissue. We know further that when

by any abnormality the amount of chromatin is increased, as when a nucleus passes through the prophases of mitosis but fails to divide, the karyolymph is proportionately increased. The characteristic phases of the nucleus, vegetative and mitotic, are marked off from each other principally by the appearance and dispersal of the karyolymph. Indeed, it is a general rule that whenever the karyolymph is absent, the anabolic activity of the cell is suspended. The characteristic condensed condition of sperm nuclei is another illustration. The shriveling of the nuclei of the resting spores in *Rhodochytrium* above described is due to the partial disappearance of karyolymph when growth ceases and the dormant period is entered upon.

SEGMENTATION.—In regard to the process of segmentation, the uncertainties encountered in *Rhodochytrium* are largely duplicated in *Synchytrium*. HARPER (12) reported that segmentation occurs by the formation of cleavage furrows, which begin to penetrate the cytoplasm at a relatively early stage in the multiplication of the nuclei. KUSANO (18) found that while some cysts undergo progressive cleavage, as described by HARPER, others show simultaneous segmentation by the precipitation of membranes around the segments. My own observations, like KUSANO'S, showed both of these methods of segmentation, but in my material the progressive cleavage described by HARPER was infrequent. The apparent duplication of segmentation recalls the double contraction reported in various phycomycetes and certain algae, such as *Hydrodictyon* (KLEBS 14, TIMBERLAKE 30). But it is not easy to correlate the accounts of observations on living and on fixed material, and for that reason the writer finds himself unable to interpret the phenomena satisfactorily.

Alga or fungus?

Having examined the morphology and cytology of the plant, we may proceed to consider its relationships. Since it is an obligate parasite without chlorophyll, one naturally wonders how it was ever referred to the protococcoid algae. On a superficial examination certainly, it would appear that the plant is no alga but a chytrideaceous fungus. The first question that arises, therefore, is

whether *Rhodochytrium* is an alga or a fungus. As will be seen, the answer depends not so much upon any interpretation of the facts of the case, as upon the point of view of the student.

Among the Chytridiales, *Entophlyctis*, of the family Rhizidiaceae, is strikingly similar to *Rhodochytrium* in gross morphology. Both are characterized by an external button connecting by a narrow neck with the main body of cyst. The rhizoidal system, if not exactly of the same appearance in the two cases, is of the same type, and the differences may be supposed to be due to the character of the substrata, which in one case is the soft protoplast of an alga and in the other the tough vascular bundle of a seed plant. The life cycles are identical; both start from a free swimming zoospore that penetrates the host, giving rise to an internal ampulla which on maturity becomes either a resting spore or a zoosporangium. Altogether *Entophlyctis* is so similar to *Rhodochytrium* that the comparison is exceedingly suggestive.

Nevertheless, there does not seem to me to be any good reason for connecting *Rhodochytrium* and *Entophlyctis*. The comparative anatomy of the Rhizidiaceae would seem distinctly to forbid such an idea. Within the family Rhizidiaceae there are apparently all transitions from purely epiphytic parasites with as little penetration as possible, to complete endoparasites. At the beginning of the series may be placed *Rhizophidium brevipes*,[4] which barely penetrates the wall of its host, without putting out any rhizoids to gather nutriment. Further stages are shown by various species of *Phylactochytrium*, which not only have extensive rhizoids, but develop a small basal portion of the plant body itself within the host. In *P. equale* the internal portion of the body becomes as large as the external. From this condition it is an easy step to *Entophlyctis* by the enlargement of the internal portion at the expense of the external, with consequent transference of the sporogenous function. This has every appearance of being a natural phyletic series. In it the parasitic mode of life would appear to

[4] *Harpochytrium* is even more surely an epiphytic parasite, since it does not penetrate its host at all, being merely attached to its wall; but it is not used in the present comparison because its relationships have been subject to some difference of opinion among different observers. WILLE (33), for example, believes that it is a colorless member of the Protococcoideae.

have been developed from an epiphytic ancestry, while endophytism did not appear until later.

In contrast with this group, *Rhodochytrium* seems to have been derived from organisms which acquired the endophytic habit of life before any real dependence on their hosts was established.

Moreover, the zoospores of *Rhodochytrium* appear to differ fundamentally from those of the Chytridiales. In most of the latter there is but one flagellum, which is often trailed along behind and imparts a weak jerky motion to the spore. In the genera with biflagellate zoospores the flagella, in most cases at least, are of the same type, and usually spring from different portions of the body.[5] Sometimes also the spores put out pseudopodia and move about in amoeboid fashion. In *Rhodochytrium* the zoospores are capable of no such motion, but maintain the integrity of their shape with slight variation throughout their period of activity. The cilia, which are anterior, are more highly specialized structures and maintain a rapid vibration which propels the spore with the steady motion characteristic of algal zoospores in general, to which those of *Rhodochytrium* correspond in every important particular, save in the absence of chlorophyll.

But the nature of the parasitism of *Rhodochytrium* indicates a very considerable degree of departure from the algae. An obligate parasite which has established definite relations with specific hosts, even though its different races show no morphological modification, is certainly far from a typical alga. The loss of plastids is an important characteristic of the fungi, but the presence of starch grains looks back toward the algae. Though starch has been reported in several fungi, and some of them contain certain carbohydrates which give the starch reaction with iodine, such as starch cellulose ("lichenin"), there is no well authenticated instance of the occurrence of definite grains of starch in any undoubted fungus.

Turning now to the algae along the lines suggested by LAGERHEIM's paper, we find among the protococcoid algae a number of

[5] In a paper to be published almost concurrently with this (Ann. Botany, January 1912), the proof of which I have seen through the kindness of the author, Dr. J. T. BARRETT, it is shown that the zoospores of several species of *Olpidiopsis* have two flagella *springing from the same point*, while other species of the same genus are reported as uniflagellate.

very interesting endophytes or "*Raumparasiten*," which have been made known principally by the researches of KLEBS (13). The climax of this series is found in *Phyllobium dimorphum*, which penetrates dying leaves of *Lysimachia nummularia*. Its adult body is strikingly similar to that of *Rhodochytrium*. There is a long empty neck, with an external cellulose button connecting the internal cyst with the wall of the zoospore from which it developed, just as in *Rhodochytrium*. In its most typical development this plant is confined to the vascular bundles of its host, into which it penetrates very much as does *Rhodochytrium*. It sends out, moreover, numerous interlacing rhizoids, which follow along the bundles for considerable distances, and even extend up their branches. On germination the resting cysts give rise to biciliate zoospores which conjugate as in *Rhodochytrium*, except that there is a slight sexual differentiation, microzoospores and megazoospores being formed in different cysts. The cysts and the zoospores have abundant chlorophyll, but haematochrome is also present in considerable amounts in some stages of the life cycle. Little is known of the finer structure or cytology[6] of this plant, but, so far as one can judge from the evidence available, it is remarkably close to *Rhodochytrium*. The most important difference between them would seem to be the presence of chlorophyll in the one and its absence in the other. OLTMANNS (21, pp. 322 ff.) believes that these forms belong to a natural series. He agrees with LAGERHEIM that *Rhodochytrium* is an alga, saying "while the first named genus [*Phyllobium*] cannot be considered more than an endophyte, as we have already clearly demonstrated, *Rhodochytrium* is one of the rare examples of an alga which has lost its chlorophyll on account of parasitism."

It will be seen, therefore, that the decision as to whether *Rhodochytrium* is an alga or a fungus depends upon the criteria by which the line between them is to be drawn. If the question is to be settled by definition, we should follow VUILLEMIN (32) and call it a fungus, for it would be very difficult to frame a definition of the fungi which would exclude *Rhodochytrium*. This position is also

[6] OLTMANNS states, on the basis of unpublished observations by GRUEBER, that the cyst is uninucleate.

taken by LINDAU (20), who excludes it from the algae on account of the absence of chlorophyll. If, on the other hand, the matter is to be decided by the relationships of the plant, it is clear that since its nearest affinities are with undoubted algae, *Rhodochytrium* must be considered an alga. It is not a matter of great consequence whether such an organism is considered a fungus or an alga, so long as its real affinities are recognized. But in the case of *Rhodochytrium* it will probably be more convenient to consider it with the algae than with the fungi, since it can be satisfactorily approached only from the algal side.

Evolutionary inferences

But although *Rhodochytrium* is to be considered the extreme of an algal series and not a near relative of any of the Archimycetes, the phyletic position of the Phyllobiae, taken as a whole, remains to be considered. We have here a series of endophytes culminating in a colorless parasite. Does this line of evolution end blindly, or do these forms furnish the clue to the origin of some fungal group? Nearly forty years ago, before *Phyllobium*, *Rhodochytrium*, and *Endosphaera* were discovered, COHN (6) recognized the general similarity of his newly discovered *Chlorochytrium* to *Synchytrium*, and suggested that the two were phylogenetically connected.

There are now known far more points of similarity in gross morphology between the different genera of the Phyllobiae and *Synchytrium* than those which induced COHN to make the comparison. Indeed, could one construct a plant with a combination of characters from the different genera, he would have a very satisfactory transition to *Synchytrium*. Such a hypothetical plant would be an obligate parasite definitely limited to specific hosts, like *Rhodochytrium*. But it would have no rhizoids, retaining rather the simple spheroidal form of *Chlorochytrium* and *Endosphaera*. It would have simultaneous segmentation like *Rhodochytrium*, but the segments would become sporangia rather than zoospores, as in *Endosphaera*, which has substantially the same method of reproduction as *Synchytrium*, except that the swarmers conjugate, while in *Synchytrium* no sexual process is known. It would have lost its plastids, and instead of having chlorophyll

would be pigmented with haematochrome. Should such a plant be discovered, the probabilities are that it would be placed in the Synchytriaceae rather than among the Phyllobiae, where by hypothesis it belongs.

But it must be recognized that the comparison fails utterly at certain points. The germinating zoospore of *Synchytrium* does not form an external button on the surface of its host, and the zoospores are of different types, as shown above. These matters are regarded by some as fundamental criteria of relationship. PETERSEN (23) considers that the presence of an external button in the Chytridiales is clear evidence that they have originated from the filamentous Phycomycetes. But this contention would lose its force if applied to *Chlorochytrium* and *Rhodochytrium*, for these would hardly be regarded by anyone as reduced Siphomycetes. The number of flagella borne by the zoospores is used as a fundamental basis of classification by LOTSY and by VUILLEMIN (32), who regard the genera with biflagellate zoospores as entirely distinct from the other Archimycetes, and classified with them merely because of accidental similarities in form, using as an example *Myzocytium*, which, however, appears distinct from the Chytridiales for other reasons as well. But the Javanese genus *Woroninella* was separated from *Synchytrium* almost entirely on account of the possession of biflagellate zoospores. In all other characters, including the large primary nucleus, it seems to be exceedingly close to *Synchytrium*. Our present information concerning *Woroninella*, which is all contained in a brief description without figures (RACIBORSKI 24), is too meager to enable us to judge whether it is transitional between *Rhodochytrium* and *Synchytrium*. But the description of *Woroninella* goes far to remove those objections to connecting the two that are based on the differences in the zoospores (see also footnote p. 163).

As has been pointed out above in the detailed cytological comparisons, there are some very striking resemblances in cytology between *Rhodochytrium* and *Synchytrium*. Some of these are peculiar to the two genera, being unknown in other organisms. The most conspicuous and perhaps the most significant of these is the enormously overgrown primary nucleus. It is evident that

these are truly unicellular organisms devoid of nuclear as well as cell division until the beginning of the reproductive period. The single cell which composes the plant body does not show any notable specialization in its cell organs, but it reaches a size which is exceeded only by a very few of the largest infusorians, while no nuclei of anything like equivalent size are to be found elsewhere among the Protista. The resemblances in these primary nuclei are not merely superficial, but are emphasized by detailed comparisons of their structure. Though their mitoses differ somewhat in detail, they also are certainly analogous in many respects.

These cytological resemblances, coupled with the general similarity in gross morphology and the tendency toward parasitism so evidently manifest in the Phyllobiae, are certainly very suggestive. It is difficult to imagine that such peculiar cytological features originated independently. If the cytology of the other members of the Phyllobiae and of the genera closest to *Synchytrium* should fall into line with the evidence now available in *Rhodochytrium* and *Synchtrium*, it would make a strong case in favor of a phyletic relationship between the two groups. But it would afford no reason for supposing them *closely* related, for *Synchytrium* appears to occupy an isolated position. The gap which separates it from Phyllobiae would appear to be of ordinal rank, and, at the same time, it is generally recognized that it is far from most other Archimycetes. Nor would it show that *Synchytrium* was derived directly from *Rhodochytrium* or even from Phyllobiae. But it would indicate that these forms may serve as a guide post pointing out the most probable location of the evolutionary path followed by the ancestors of *Synchytrium*.

Summary

Rhodochytrium does not appear in North Carolina until late in the spring; at first zoosporangia are most abundant, but late in the season only resting spores are found.

The cysts are independent, not connected through their rhizoids.

The zoospores are of the algal type and frequently contain starch grains, but are colorless except for the red anterior end; they are

active for half a day or more, but seem to conjugate rarely except when confined in small amounts of fluid.

The nature of the cyst (resting spore or zoosporangium) is determined on infection.

The red pigment which is found at all stages of the life cycle is haematochrome or an allied lipochrome.

Although the three races of *Rhodochytrium* appear to be geographically isolated and affect different hosts, no morphological differences were detected between them.

The germ tubes do not enter the stomata, but penetrate the epidermis at any point, usually in the vicinity of a vascular bundle.

The cysts, both resting and temporary, are uninucleate until full size is attained.

Their rhizoids extend along the vascular bundles, mostly in the phloem elements, which they destroy, but they also send haustoria to the vessels of the xylem.

When mature the resting spores have a two-layered cellulose exospore and a thick non-cellulose endospore; most of the reserve food is in the form of starch; the nuclei are considerably shriveled by the withdrawal of karyolymph.

The starch grains are similar to those commonly seen in the higher plants.

No plastids could be found, the starch grains appearing to be built up directly in the plasma.

The flaring necks of the zoosporangia are stopped by characteristic turbinate or bell-shaped plugs.

During the last mitoses there is a contraction which results in a pseudo-segmentation, but true segmentation appears to be brought about by the precipitation of membranes around the protospores.

There is a deeply staining body at the base of the cilia of the zoospores which is connected with the nucleus.

The primary nuclei, which reach the size of 50–60 μ, have enormous nucleoli and peculiar amorphous masses of chromatin like *Synchytrium decipiens*.

In the first type of mitosis, the spindle, which is usually unipolar at first, is formed from coarse acicular fibers that appear within

the nuclear cavity; it has no connection with the nuclear membrane. The spirem is formed from that part of the chromatin which lies in the equatorial region, the rest being cast out; it is frequently entirely within the spindle.

The second type of mitosis presents no unusual features.

No centrosomes or true asters were seen.

Amitosis is rare and abnormal in the zoosporangia.

Although superficially resembling *Entophlyctis*, *Rhodochytrium* is not closely related to any known Archimycete.

But it appears to be closely related to the Protococcoideae through *Phyllobium*.

The Phyllobiae show considerable similarity to *Synchytrium* in gross morphology.

The cytology of *Rhodochytrium* bears a strong resemblance to that of *Synchytrium*.

These resemblances suggest that *Synchytrium* was derived from protococcoid ancestors.

OHIO STATE UNIVERSITY
COLUMBUS, OHIO

LITERATURE CITED

1. ATKINSON, GEO. F., A parasitic alga, *Rhodochytrium spilanthidis*, in North America. BOT. GAZ. **46**:299–301. 1908.
2. ——, Note on the occurrence of *Rhodochytrium spilanthidis* in North America. Science N.S. **28**:691–692. 1908.
3. ——, Some problems in the evolution of the lower fungi. Ann. Myc. **7**:441–472. *figs. 20.* 1909.
4. ——, Some fungus parasites of algae. BOT. GAZ. **48**:321–338. *figs. 8.* 1909.
5. CHAMBERLAIN, C. J., The ovule and female gametophyte of *Dioon*. BOT. GAZ. **42**:321–358. *pls. 3.* 1906.
6. COHN, FERDINAND, Ueber parasitische Algen. COHN'S Beiträge **1**[2]:87–108. *pl. 3.* 1872.
7. DEBAISIEUX, PAUL, Les debuts de l'ovogenèse dans le *Dytiscus marginalis*. La Cellule **25**:207–237. 1909.
8. GRIGGS, R. F., On the cytology of *Synchytrium*. III. The rôle of the centrosomes in the formation of the nuclear membrane. Ohio Nat. **8**:277–286. *pls. 19, 20.* 1908.
9. ——, Some aspects of amitosis in *Synchytrium*. BOT. GAZ. **47**:127–138. *pls. 3, 4.* 1909.

10. GRIGGS, R. F., A note on amitosis by constriction in *Synchytrium*. Ohio Nat. **9**:513–515. *figs. 4*. 1909.
11. ———, Mitosis in *Synchytrium*, with some observations on the individuality of the chromosomes. BOT. GAZ. **48**:339–358. *pls. 16–18*. 1909.
12. HARPER, R. A., Cell division in sporangia and asci. Ann. Botany **13**:467–525. *pls. 24–26*. 1899.
13. KLEBS, G., Beiträge zur Kenntnis niederer Algenformen. Bot. Zeit. **39**:248–257, 265–272, 281–290, 297–308, 313–319, 329–336. *pls. 3, 4*. 1881.
14. ———, Fortpflanzenzellen bei *Hydrodictyon utriculatum* Roth. Bot. Zeit. **49**:789. 1891.
15. KUSANO, S., On the nucleus of *Synchytrium puerariae* Miyabe. Bot. Mag. Tokyo **21**:118. 1907.
16. ———, On the cytology of *Synchytrium*. Centralbl. Bakt. **19**²:538. 1907.
17. ———, On "karyodermatoplast," a nuclear membrane-forming body (in Japanese). Bot. Mag. Tokyo **22**:205–206. 1908.
18. ———, A contribution to the cytology of *Synchytrium* and its hosts. Bull. Col. Agr. Imp. Univ. Tokyo **7**:80–147. *pls. 8–11*. 1909.
19. LAGERHEIM, G., De *Rhodochytrium*, nov. gen. Eine Uebergangsform von den Protococcaceen zu den Chytridiaceen. Bot. Zeit. **51**:43–53. *pls. 2*. 1893.
20. LINDAU, G., In ENGLER and PRANTL'S *Pflanzenfamilien*, Nachtr. zu **1**¹:528. 1900.
21. OLTMANNS, FRIEDERICH, Morphologie u. Biologie der Algen. **2**:322. Jena. 1905.
22. PERCIVAL, JOHN, Potato wart disease; the life history and cytology of *Synchytrium endobioticum*. Centralbl. Bakt. **25**²:440–447. *pl. 3*. 1909.
23. PETERSEN, H. E., An account of Danish fresh water Phycomycetes, with ecological and systematical remarks. Ann. Myc. **8**:494–560. 1910.
24. RACIBORSKI, M., Pflanzenpathologisches aus Java. Zeitschr. f. Pflanzenkrank. **8**:195–200. 1898.
25. SALTER, J. H., Zur naehere Kenntniss der Staerkekoerner. Jahrb. Wiss. Bot. **32**:117–165. *pls. 1, 2*. 1899.
26. STRASBURGER, E., Ueber den Bau und das Wachstum der Zellhaute. pp. 155 ff. Jena. 1888.
27. ———, Ueber Reduktionstheilung, Spindelbildung, Centrosomen, und Cilienbildner im Pflanzenreich. Hist. Beitr. **6**: Jena. 1900.
28. STEVENS, F. L., Some remarkable nuclear structures in *Synchytrium*. Ann. Myc. **5**:480–484. *pl. 13*. 1907.
29. STEVENS, F. L., and A. C., Mitosis in the primary nucleus of *Synchytrium decipiens*. BOT. GAZ. **35**:405–415. 1903.
30. TIMBERLAKE, H. G., Starch formation in *Hydrodictyon utriculatum*. Ann. Botany **15**:613–635. *pl. 34*. 1901.
31. ———, The development and structure of the swarm spores of *Hydrodictyon*. Trans. Wis. Acad. **13**:486–522. *pls. 29, 30*. 1902.

32. VUILLEMIN, PAUL, Les bases actuelles de la systematique en Mycologie. Prog. Rei Bot. 2:40–170. 1907.

33. WILLE, N., Nachtrage zu Chlorophyceae in ENGLER and PRANTL's *Pflanzenfamilien*, Nachtr. zu 1²:48–49. 1909.

EXPLANATION OF PLATES XI–XVI

The figures were made with various combinations of Zeiss apochromatic and Spencer achromatic oil immersion lenses with compensating oculars. The magnification of the different figures is given in the description of each. The figures have been reduced one-third in reproduction, canceling the enlargement due to the camera and rendering them the same size as when seen in the microscope. All of the figures, except 16 and 19, were taken from the race of the parasite on *Ambrosia artemisiifolia*.

FIG. 1.—Young resting spores; ×334.

FIG. 2.—Somewhat older resting spore, spreading out irregularly in the tissue; ×334.

FIG. 3.—Cyst in which the basal portion has swollen out, although the protoplast has grown but little; rhizoids not in plane of section; nucleus with numerous spherules of chromatin connected by linin strands scattered through its cavity; ×334.

FIG. 4.—A full-sized resting spore whose wall is beginning to thicken, with that portion of the rhizoidal system which lay in the plane of section; ×334.

FIG. 5.—A portion of the rhizoidal system of a mature cyst, showing its relation to phloem and xylem; ×334.

FIG. 6.—Detail of a haustorium closely applied to a pitted vessel; from a cyst which had surrounded itself with a thick wall, hence the wall around the haustorium; ×334.

FIG. 7.—Two-layered resting spore, showing the shriveling of the nucleus and the cutting off of the rhizoids; ×334.

FIG. 8.—Mature three-layered resting spore; ×334.

FIG. 9.—Starch grains from mature cysts, showing variations in size and shape; ×2000.

FIG. 10.—Starch grains from a mature cyst under polarized light; ×2000.

FIG. 11.—Young zoosporangium with numerous fine strands of cytoplasm in which starch is forming; ×334.

FIG. 11*a*.—Detail from fig. 11, showing formation of starch grains; ×3000.

FIG. 12.—Young zoosporangium; ×334.

FIG. 13.—Young zoosporangium just beginning to swell out; ×334.

FIG. 14.—Young zoosporangium in the stem of the host; plug already developed, although the tubular form is still retained; ×334.

FIG. 15.—Full-sized zoosporangium, showing the characters of the primary cyst; ×334.

FIG. 16.—A typical turbinate plug from the race on *Asclepias pumila*; ×670.

FIGS. 17, 18.—Lamellate plugs; ×670.

FIG. 19.—An unusual form of lamellate plug from the race on *Spilanthes;* ×670.

FIG. 20.—A bell-shaped plug, apparently secondarily filled up; ×670.

FIG. 21.—A bell-shaped plug which is perforate; ×670.

FIG. 22.—A binucleate cyst with part of its rhizoids showing by a starch-free area the approximate size and position of the primary nucleus and the remains of the residual chromatin cast out during the primary mitosis; ×334.

FIG. 23.—The tetranucleate stage; drawn from two sections of a retort-shaped cyst with the bend perpendicular to the plane of section; the sporangium, and especially the vacuole, were therefore larger than is indicated in the drawing; ×334.

FIG. 24.—An 8-nucleate cyst in which the position of the primary nucleus is still clearly indicated by a starch-free area in the cytoplasm; only six nuclei in plane of section; ×334.

FIG. 25.—An oblique section of 16-nucleate cyst in which the nuclei were still bunched in the center; ×334.

FIG. 26.—A small cyst in the 32-nucleate stage; ×334.

FIG. 27.—A cyst with about 128 nuclei; ×334.

FIG. 28.—A segmented zöosporangium, the protospores still retaining the shape of the coenocyte from which they were derived; ×334.

FIG. 29.—A cyst apparently segmenting by cleavage furrows; ×1000.

FIG. 30.—Preliminary contraction resulting in pseudo-segmentation during the last mitoses; ×1000.

FIG. 31.—Segmentation by the precipitation of membranes in the cytoplasm: *a*, a wall just forming; *b*, a portion of cytoplasm left out between the segments; ×1000.

FIG. 32.—A newly formed protospore; ×2000.

FIG. 33.—A protospore rounded off and beginning to show the concentration of the chromatin; ×2000.

FIG. 34.—A protospore overstained, showing the body at the base of the cilia and its connection with the nucleus; ×2000.

FIG. 35.—A young spore with starch grains partly concentrated in the posterior end; chromatin concentrated into a single mass; ×2000.

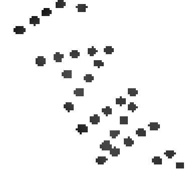
FIG. 36.—Mature spore from a section showing basal body and antero-posterior differentiation of the spore; ×2000.

FIG. 37.—Free swimming zoospore killed with osmic fumes stained with gentian-violet; ×1000.

FIGS. 38–41.—Stages in the conjugation of the zoospores from living material; cilia diagrammatic; the difference in size between the gametes was accidental; there is no differentiation into microgametes and megagametes.

FIG. 42.—A nucleus from a very young cyst; ×2000.

FIG. 43.—A nucleus from a young resting spore; vacuolation of karyosome beginning; few connections between the chromatin spherules; ×2000.



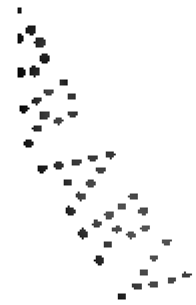


FIG. 44.—A n
...e central vac
...d developed;
FIG. 45.—En
FIG. 46.—A
FIG. 47.—A
single central
FIG. 48.—T
the other thre
FIG. 49.—
FIG. 50.—
opposite pole
FIG. 51.—
pole of the s
FIG. 52.—
division; ×
FIG. 53
residual ch
aster at or
FIG. 5
completel
FIG.
fourth di
FIG.
FIG.
nucleus
FIG
partly
FI
FI
from
F
pro

FIG. 44.—A nucleus f
single central vacuole; co
well developed; ×2000.
FIG. 45.—Enlarged dr
FIG. 46.—A nucleolus
FIG. 47.—A nucleolus
a single central vacuole; ×
FIG. 48.—The beginn
the other three nuclei wer
FIG. 49.—Early proph
FIG. 50.—Later propl
opposite pole could be fou
FIG. 51.—Prophase in
pole of the spindle and o
FIG. 52.—Late proph
division; ×2000.
FIG. 53.—Metaphase
residual chromatin, and i
aster at one pole largely
FIG. 54.—Metaphase;
completely segmented int
FIG. 55.—Anaphase, s
fourth division; ×2000.
FIG. 56.—Early telopl
FIG. 57.—Late teloph
nucleus; first division; ×
FIG. 58.—Late proph
partly finely divided; ×2
FIG. 59.—Metaphase
FIGS. 60, 61.—Resting
from the same cyst; ×20
FIG. 62.—Metaphase,
FIGS. 63–66.—Teloph
FIGS. 67, 68.—Cysts
products of amitosis; ×3

AMERICAN TRIASSIC NEOCALAMITES

EDWARD W. BERRY

(WITH PLATE XVII AND ONE FIGURE)

One of the most dogmatic statements of geology and paleontology refers to the almost complete change in the character of the floras in passing from the Paleozoic to the Mesozoic. This is a venerable dogma handed down from generation to generation until it has become almost axiomatic. Nevertheless, like most dogmas both scientific and otherwise, it was originally based upon lack of knowledge and its chief attribute is its unsoundness. A second misconception of a narrower kind is the current belief that the rocks of the Richmond coal-field in Virginia are of Keuper age. This latter seems to be based upon STUR's comparison (7) with the Lunzer Lettenkohl flora of Austria, and upon the somewhat naïve reasoning of SHALER (6) that since the continued flora, whose affinities were early recognized, is unmistakably Rhaetic in its facies, it therefore is not of Rhaetic age, since it must have taken it untold years to spread over the world. This is an extreme application of HUXLEY's principle of homotaxis, which is entirely unwarranted, and one which will be referred to again.

With increasing knowledge it has become obvious that one of the main reasons for the floral break at the close of the Paleozoic is conditioned by the unfavorable character of the early triassic sedimentation for preserving plant fossils. Among the forms which pass the magic boundary are *Glossopteris*, a probable pteridosperm, as WHITE (9) and others have pointed out; *Yuccites*, *Noeggerathiopsis*, *Krannera*, *Eolirion*, and *Cardiocarpon*, and possibly other more or less indefinite fossils may represent the Cordaitales in the older Mesozoic, as ZEILLER (12) has recently suggested. *Sigillaria* is represented by the form which was christened *Pleuromeia* by CORDA.

A number of genera of cycadophytes are already differentiated in the late Paleozoic, and it has long been evident that, in spite of the contrary tradition, the triassic Equisetales are more like their paleozoic than their existing representatives.

HALLE (3) has recently suggested setting aside certain species formerly referred to the illy understood equisetaceous genus *Schizoneura*, to constitute a separate and perhaps collaterally related genus, for which he has proposed the name *Neocalamites*, and which he compares with the paleozoic *Calamites*. WILLS (11) has supplemented this suggestion by comparing the species which are left in the genus *Schizoneura* with GRAND'-EURY'S *Calamodendron* type of paleozoic *Calamites*, and LIGNIER (5) has recently described *Calamitomyelon Morierei* from the French Lias.

The previously known species of *Neocalamites* are three in number: *N. meriani* (Brongn.), *N. hoerensis* (Schimper), and *N. carrerei* (Zeiller), and all are Keuper or Rhaetic in age. Both this genus and *Schizoneura* have been discussed by WILLS (10, 11) since the appearance of HALLE'S paper, so that further comments are unnecessary.

In an examination of the recently reopened Carbon Hill mine in the Richmond coal-field of Virginia, two equisetaceous types were discovered which are apparently referable to *Neocalamites*. The one, represented by very abundant but exceedingly poor remains, is identified with *Schizoneura virginiensis* described from this area in 1883 by FONTAINE (2). This represents a species which appears to be very close to *Schizoneura meriani* Brongn., and consequently referable to *Neocalamites* as defined by HALLE. It is described by FONTAINE as having several very fine veins, but this character is very obscure in all of the material and may or may not be true. It is something more than a coincidence that a like state of affairs seems to prevail in *S. meriani* described ordinarily as uninerved, but which WILLS has found to sometimes show several fine median veins. The other is an entirely new and remarkable type, which, in its superficial features at least, is very suggestive of the paleozoic *Calamites* with the *Annularia* type of foliage. The two were not found associated, although according to the mine engineer they both came from the same level, that is, the roofing shales of the 6-foot seam. The specimens were collected from the dumps, and their contemporaneous growth should therefore be accepted with caution, since the facies of the plants associated with each is slightly different, but probably equally explicable

either by a slightly different environment or by their having come from a somewhat different level. The dumps from which collections were made represent two openings: the eastermost of which is a slope mine following the dip of the 6-foot seam which comes rather close to the surface near the entrance; the westermost, 200 yards away, known as the Engine Hill mine, is a shaft which was said to strike the same 6-foot seam at a depth of 250 feet, but which was not being worked at the time of the writer's visit. *Neocalamites virginiensis* (Fontaine), as it should be called, was collected from the eastern dump, where it was associated with vast numbers of fronds of *Macrotaeniopteris magnifolia* (Rogers) Schimper, and with the equally abundant stem remains of large and small specimens of *Equisetum* and very rare fern fragments, the whole constituting a typical triassic swamp assemblage.

In the flora associated with the new species of *Neocalamites* the remains of *Equisetum* were almost entirely absent, *Macrotaeniopteris* was not seen, and ferns and cycadophytes greatly predominated. The pinnules of the enormous *Sphenozamites Rogersianus* Fontaine were often packed together in solid masses, among which some nearly complete fronds were collected. *Clathropteris* was common and some of the specimens were remarkably complete. The fern genera identified by FONTAINE as *Acrostichides*, *Mertensides*, etc., were abundant, and various *Ctenis*-like and *Pterophyllum* forms were collected. Sparingly represented were those curious forms described by EMMONS (1) over 50 years ago from the North Carolina Triassic area under the name *Lepacyclotes*.

EMMONS (1) described two species in 1856 as *Lepacyclotes ellipticus* and *L. circularis*. These were discussed by FONTAINE (2) in 1883 in his monograph of the Virginia Triassic. At that time he considered them as probably representing a single species of crushed cone closely allied to *Araucaria*, and they were renamed by him *Araucarites carolinensis*. In returning to the same subject in 1900, after the rediscovery of the EMMONS' collection, he abandons this view and returns to EMMONS' names, his final opinion being that the disklike forms represent *Equisetum* diaphragms, and the scalelike forms fragments of *Equisetum* stems (8). I am not in a position to discuss the first assumption, since I have not seen the

material. The second is clearly erroneous. The Virginia specimens are cone scales, and while it is merely a supposition, I would be inclined to consider them as representing contemporaneous cycadophytes rather than Araucarieae.

The new species of *Neocalamites* was collected by the writer and T. E. WILLARD of the U.S. National Museum, and is named in honor of Dr. F. H. KNOWLTON, who was instrumental in bringing about the writer's visit to the mine.

Neocalamites Knowltoni, sp. nov.

The main axis is preserved for a distance of 14 cm., and shows 8 nodes in this interval. It is slender, being 8 mm. across the flattened proximal end, and 6 mm. across the flattened distal end. The nodes are about 2 mm. apart, and show no traces of leaves or sheaths. The surface is lined longitudinally, and there is no apparent alternation of vascular strands at the nodes, a variable feature in this whole class of plants and much less important than was formerly supposed to be the case. Leaf-bearing branches opposite. They were possibly in whorls in some cases, since there appear to be 1 or 2 branch scars just above certain of the nodes, which, if they indicate fully developed branches in addition to the two opposite ones which are preserved, would make the leaf-bearing branches 3 or 4 in number at these respective nodes. It is believed, however, that the functional branches were usually but 2 in number and opposite, since no traces of additional branches are preserved. If other branches developed occasionally, they may be regarded as reversions to an ancestral verticillate arrangement, and the branch scars above mentioned may be interpreted as the scars of such aborted or non-persistent branches.

Lateral foliage-bearing branches preserved for a length up to 7 cm., slender, being not over 3 mm. across at the proximal end after flattening due to the compression of fossilization. Internodes short, about 1 cm. in length, longitudinally striated.

Leaves in whorls of 9 or 10 at the nodes of the lateral branches, apparently free, although they may be slightly united at the base as in the paleozoic Annularias, the material collected being not entirely conclusive on this point. They are linear-lanceolate in

outline, with an obtusely pointed apex, about 1 cm. in length by 1.5 mm. in greatest width. All the leaves in a whorl are of approximately the same size.

From their position as fossilized, they seem to have been superimposed from node to node, and each verticil seems to have been in a plane very oblique to the supporting axis and not at right angles to it, so that the foliage-bearing branch with its unit whorls is, as a whole, bifacial.

Leaf substance thick and coriaceous. Within the limits of the specimen there is scarcely any diminution in the size of the leaves or length of the internodes distad from the main axis, although the branch itself tapers slightly.

The venation is puzzling because of the thick nature of the leaves and their indifferent preservation, some leaves apparently showing a thick prominent midrib, while in others its place was apparently occupied by what seem to be several very fine vascular strands.

FIG. 1

The writer's final conclusion is that each leaf has a single midrib, which was broad, but immersed in the leaf substance and not at all prominent in life. This midrib may have been made up of several vascular strands, and varying conditions of preservation account for the deceptive appearances in some of the leaves.

The accompanying text figure (fig. 1) is from a drawing (×4) which shows three verticils, and is drawn from a counterpart of the type which is shown natural size on pl. XVII.

In the absence of any very complete knowledge of the older mesozoic Equisetales, the affinities of the present species are more or less conjectural. It fulfils all of the requirements of HALLE's definition of the genus *Neocalamites*, and the genus itself seems to be a natural one. It is more like *Calamites*, however, than the species which HALLE has referred to the genus, and suggests most strongly the *Annularia* type of paleozoic calamite foliage, as, for example, the widespread type known as *Annularia sphenophylloides*, the only difference being that in the triassic *Neocalamites* the leaves

of a whorl are not dissimilar in size. A second possible difference is that the leaves appear free to the base. This is not positively ascertained, however, and is of slight importance at best, since there must have been a progressive change from free leaves to united sheaths and vice versa, when the group as a whole is considered, and the two lines of variation may have been contemporaneous within the phylum.

There is also a suggestive resemblance between the present species and the forms from the homotaxial Rhaetic deposits of Tonkin described by ZEILLER (13, p. 132. *pl.* 35. *figs.* 2–7) as *Annulariopsis inopinata*, gen. et sp. nov. This remarkable form, while based upon rather incomplete material, shows whorls of 16–24 lanceolate-spatulate, uninerved, free leaves, the main difference betwen it and *Neocalamites Knowltoni* being the uniform size of the leaves of the latter. In *Annulariopsis* each whorl shows short leaves on one side and long leaves on the opposite side, with a regular gradation between the two, the maximum being 100 per cent larger than the minimum.

It appears, therefore, that as regards habit and superficial characters *Neocalamites* was closely allied to and undoubtedly descended from some paleozoic *Calamite*. On the other hand, it does not seem to be genetically related to *Schizoneura*, although it comes after it in time.

Neocalamites Knowltoni was a large plant, and it is quite possible that some of the fragments of large stems 10 or 12 cm. in diameter, which are so abundant at some horizons in the coal-field, may represent the main axis. The axis of the specimen, with its leaf-bearing subordinate branches, is interpreted as a lateral branch which was distinctly bifacial in habit. The material from the Triassic is too limited for certainty on this point, but it seems difficult to account for the uniform orientation of the numerous whorls of leaves on the distichous branches by appealing to compression during fossilization, which it would seem reasonable to suppose on even a single specimen would flatten some leaves in one direction and some in another and would break off or bend some of the leaves.

The obliquity of the plane of the verticils in *Annularia* is often insisted upon in the diagnosis of this paleozoic type, although some

authors explain this feature by compression during fossilization. In this case also the mechanical orientation of the *Annularia* whorls in the thousands of specimens which have been collected is difficult if not impossible of adequate explanation if the theory that the leaves in life radiated at right angles to the axis be adopted. The present specimen comes from the immediate vicinity of the old Carbon Hill mine, about one mile south of Gayton on Tuckahoe Creek, near the western border of Henrico County, Virginia, from beds of undoubted Rhaetic age, and the type is deposited in the U.S. National Museum, duplicate and less perfect material being retained in the collections of the Johns Hopkins University.

JOHNS HOPKINS UNIVERSITY
BALTIMORE, MD.

LITERATURE CITED

1. EMMONS, E., Geol. rept. of the midland counties of North Carolina. Raleigh. 1856.
2. FONTAINE, W. M., Contribution to the knowledge of the older mesozoic flora of Virginia. Monograph U.S. Geol. Surv. **6**:1883.
3. HALLE, T. G., Zur Kenntnis der mesozoischen Equisetales Schwedens. Kgl. Svenska Vetens.-Akad. Handl. **43**:pp. 56. *pls. 9.* 1908.
4. KRASSER, F., Zur Kenntnis der fossilen Flora der Lunzer Schichten. Jahrb. Geol. Reichs. **59**:101–126. 1909.
5. LIGNIER, O., *Calamitomyelon Morierei*, gen. et sp. nov. Bull. Soc. Linn. Normandie VI. **2**:116–128. *pls. 1–3.* 1908.
6. SHALER, N. S., and WOODWORTH, J. B., Geology of the Richmond Basin, Virginia. 19th Ann. Rept. U.S. Geol. Surv. II. 1899: 385–520.
7. STUR, D., Die Lunzer (Lettenkohlen) Flora in den "Older mesozoic beds of the coal-field of eastern Virginia." Verh. Geol. Reichs. Wien. 1888: no. 10. 203–217.
8. WARD, L. F., with the collaboration of FONTAINE, W. M., WANNER, ATREUS, and KNOWLTON, F. H., Status of the mesozoic floras of the United States. First paper: The older mesozoic. 20th Ann. Rept. U.S. Geol. Surv. II. 1900:211–748. *pls. 21–179.*
9. WHITE, DAVID, Fossil flora of the coal measures of Brazil. III. Rept. Brazilian Coal Commission 1908:337–617.
10. WILLS, L. J., The fossiliferous lower Keuper rocks of Worcestershire. Proc. Geol. Ass. **21**:271–287. 1910.
11. WILLS, L. J., Notes on the genus *Schizoneura* Schimper and Mougeot. Proc. Cambridge Phil. Soc. **15**:406–410. 1910.
12. ZEILLER, RENÉ, Les progrès de la paléobotanique de l'ère des gymnospermes. Progressus Rei Botanicae **2**:171–226. 1907.
13. ZEILLER, R., Fl. foss. des gites de charbon du Tonkin. Paris. 1903.

CURRENT LITERATURE

BOOK REVIEWS

Vegetation der Erde

XIII. NORTH AMERICA

It is unfortunate that ENGLER and DRUDE should have decided to devote but one volume of the *Vegetation der Erde* to North America. Such a decision seems out of harmony with the rest of the work. It might have been expected that a work published in Europe would devote separate volumes to such relatively limited areas as the Carpathians, the Caucasus, the Balkan countries, and the North German heath. However, a somewhat comparable plan has been followed with regard to Africa, three volumes having already been issued, with more promised. Even in South America, a volume has been devoted to Chile and another to the Peruvian Andes. With such a plan, it is a fundamental mistake to devote but one volume to North America.[1] HARSHBERGER prepared himself as well as he could for the impossible task he was asked to undertake by years of study and by trips to all the more important phytogeographical areas of North America except Central America and the arctic region. Under the circumstances, the volume is one with which the author may be fairly well satisfied. It is a veritable mine of information, in which there may be found the chief results of the phytogeographic work accomplished upon our continent. There are many errors of detail throughout the volume, errors both of omission and of commission, and some are rather serious. To many, and especially to taxonomic specialists of local areas, these errors will loom large. To those of broader viewpoint, however, the numerous errors will be subordinate to the relatively successful completion of one of the most stupendous tasks ever undertaken by a single botanist. HARSHBERGER deserves and will receive the gratitude of all future plant geographers in our country, for he has vastly lightened their labors. They will value this work because of its helpfulness as a guide to literature, and because of its broad comparisons and generalizations; it will be for them an easy matter to correct the errors of determination or of synonymy and the mistakes in spelling that seem such grevious matters to some of the reviewers. This volume is the first of the series to appear in a tongue other than the German. It is a pleasure to congratulate ENGLER and DRUDE for their broad-minded conception in this

[1] ENGLER, A., and DRUDE, O., Die Vegetation der Erde. XIII. HARSHBERGER, J. W., Phytogeographic survey of North America. pp. lxiii+790. *map. pls 18. figs. 32.* Leipzig: Wilhelm Engelmann (also G. E. Stechert & Co. New York). 1911. *M.* 52 (subscription price *M.* 40).

matter, thus adopting a plan which ENGLER had previously adopted in the *Pflanzenreich*.

Following the preface is a German summary of the contents of the volume by DRUDE. Part I gives a survey of floristic and phytogeographic work in North America, and also a most useful bibliography. Part II contains an account of the geography and climate of the continent, together with some plant statistics. Part III has to do with the geologic evolution of the North American flora from the Cretaceous to the present. Here there are discussed the sudden appearance of Cretaceous angiosperms, and the influence of Pleistocene glaciation in the destruction of species and in the production of relict endemism. A detailed account is given of the postglacial history of our flora. To the north there has been a succession of forest types, culminating in the dicotyl forests which now generally dominate. Interesting accounts are given of recent changes in the vegetation of the coastal plain. HARSHBERGER aligns himself with those who regard the prairies as sufficiently explained by taking account of historical factors. This part closes with a description of the affinities of the North American flora and a list of phytogeographic classifications pertaining to North America.

Part IV, which comprises more than half of the volume, presents in some detail the phytogeographic regions of North America, and is accompanied by a colored map which makes it easy to follow the text. There are seven chapters, dividing the continent into as many "zones": (1) The arctic and subarctic zones; the latter is subdivided into the Labrador, Hudson Bay-Keewatin, Mackenzie, and Alaska districts. (2) The North American temperate zone, Atlantic section; subdivided into the St. Lawrence–Great Lake, Atlantic–Gulf Coast, and Piedmont-Appalachian-Ozark regions. Among the districts most fully treated are New Brunswick (based largely on GANONG's studies), the New England mountains, the Adirondacks, the New Jersey pine barrens, the coastal formations, and the various forest districts. (3) The North American temperate zone, interior xerophytic sections; subdivided into the prairie, Rocky Mountain, and Great Basin regions. (4) The North American temperate zone, Pacific section; subdivided into the Sitkan, Columbian, and Californian regions. (5) The Mexican subtropic zone and mountain regions. (6) The North American tropic zone, Mexican and Central American section. (7) The North American tropic zone, West Indian section. The illustrations are good, but are much too few to depict properly the vegetation of a continent.—HENRY C. COWLES.

NOTES FOR STUDENTS

Cecidology.—The similarity of plant galls and animal tumors is attracting the attention of workers in various parts of the world. SAUL[2] has issued a preliminary paper in which he expresses the opinion that some of the various

[2] SAUL, E., Beziehungen der Acari zur Geschwulstatiologie. Centrabl. f. Bakt., Paras., und Infekt. **59**:400–406. 1911.

cancerous growths of animals may be due to insects, and that improved technique will throw light upon the problem. He expresses regret that the progress of this line of work has been so slow, and reviews some of BEIJERINCK's works which he believes have the most important bearing on the subject. He believes that the insect (larva) secretes an enzyme which causes a proliferation of the body cells without changing their physiological function, and that this enzyme can be transferred from cell to cell. The possibility of insects being the cause of such growths in animals was taken up in Krebs Institute in Heidelberg in connection with the study of an endemic disease of rats. The rats suffered from an infectious disease causing papillose tumors, but the technique was not satisfactory in demonstrating the exact cause. The author presents a number of microphotographs of insects and sections of plant galls, which he discusses in relation to their similarity to animal tumors. He also briefly reviews the works of several authors who have expressed similar opinions.

One of the most valuable discussions concerning the character and grouping of galls is by KÜSTER,[3] who suggests a division of the galls into two groups, "histoide" and "organoide." The former includes such simple structures as cork formed about wounds, and the more complex structures such as oak galls, which, although made up of plant tissue, are unlike any of the plant organs. The latter includes the formation of roots from a leaf, those modifications of stems and leaves which are usually known as teratological structures, and those modifications of parts which are due to fungi and insects. The author discusses the modification of the leaves of the willow due to *Aphis amenticola*, the witches' brooms of the cherry, birch, and fir trees due to *Exoascus cerasi*, *E. betulinus*, and *Melampsorella caryophyllacearum*, the cone gall of *Salix caprea* which is due to *Rhabdophaga rosaria*, the leaf modifications of *Populus tremula* which are due to *Eriophyes dispar*, the formation of new roots on *Poa silvestris* due to *Cecidomyia poa*, the formation of adventitious parts on *Fraxinus ornus* and *Pteris quadriaurita* due to *Eriophyes fraxini* and *Taphrina laurencia*, as illustrating the various types of organoides. This is followed by a brief discussion of a number of insect and fungus galls which possess characters of both histoides and organoides. The author attaches no importance whatever to the cause, but bases his classification entirely on the character of the deformity without regard to the fungus or insect which produces the stimuli.

A brief but very interesting paper by HARRIS[4] shows that as vague a subject as teratology may present problems for serious investigation. His studies indicate that the anomalous fruits of *Ptelea trifoliata* are rare, the greatest variant being less than 1 per cent. Although the author states that he considers the number of pods studied entirely too small for satisfactory

[3] KÜSTER, E., Ueber organoide Misbildungen auf Pflanzen. Aus der Natur. **7**:673–685. 1911.

[4] HARRIS, T. ARTHUR, Teratological fruits of *Ptelea*. Bull. Torr. Bot. Club **38**:385–387. 1911.

conclusions, yet his paper demonstrates one of the many possibilities in this branch of cecidology.

Among the more important taxonomic papers is LEEUWEN-REIJNVAAN'S[5] fifth contribution on the galls of Java. They describe 49 different galls, 21 of which are figured. These galls are grouped with reference to the plants on which they occur, and are assigned to genera but not given specific names.

MASSALONGO[6] describes 8 new species of galls, 7 of which are due to insects and 1 to fungi.—MEL T. COOK.

Sand dune and subalpine vegetation in New Zealand.—With a sand dune area of some 300,000 acres, the question of its reclamation becomes one of national importance in New Zealand, especially since through their advance the dunes ruin much valuable land. In a previous paper by COCKAYNE, reviewed in this journal,[7] the ecological problems of these areas were discussed, and the influence of pasturing, tree cutting, and burning was noted as increasing the movement of the dunes to a marked degree. In a more recent publication,[8] the same investigator has restated many of his former conclusions, and in addition has discussed the best methods for reclaiming actively moving dunes, for protecting farm lands and other valuable areas from the encroaching sand, and for preventing the rejuvenescence of fixed dunes. The efficiency of marram grass (*Ammophila arenaria*) as a sand holder is emphasized, while the tree lupin (*Lupinus arboreus*) is found to be an excellent shrub to reinforce the grass and to act as a pioneer in the process of reforestation, which is recognized as offering the greatest permanent stability combined with the transformation of a barren and dangerous into a productive region. Some action by the New Zealand Government seems likely to result from these recommendations.

COCKAYNE and his associates have also been making a preliminary ecological survey of a mountainous area in the Southern Alps region of New Zealand.[9]
'e is Mt. Arrowsmith, 9171 ft., and it is surrounded by
ess altitude. Glaciers occur rather plentifully, and the
of much more extensive ice sheets in the past. Two
ere closely adjacent, due to differences in rainfall depend-

AAN, J. und W. DOCTERS VAN, Einige Gallen aus Java. V.
11.

Zoocecidii e fitocecidii rare o nuovi. Marcellia 10:94–97.

,. 1910.

port on the dune areas of New Zealand, their geology, botany,
artment of Lands. 4to. pp. 76. *pls. 72*. 1911. Wellington:
nent Printer.

KAYNE, L., and LAING, R. M., The Mount Arrowsmith dis-
ography and plant ecology. Trans. N.Z. Institute 43:315–

ing upon exposure to the moist westerly winds. In the more mesophytic region, with an annual rainfall of about 250 cm., a rain forest formation develops, its conspicuous trees being *Podocarpus Hallii*, *Librocedrus Bidwillii*, and two species of *Phyllocladus*.

In the more xerophytic portion of the region, while the precipitation is quite considerable, exposure to strong insolation and almost continuous winds produces a steppe formation. This is developed upon several sorts of rocky substrata, and is characterized by an abundance of shrubby, tussock, and cushion plant forms. The succession in some stony river beds has been more carefully studied,[10] and may indicate the interesting results likely to follow more detailed investigation of other similar situations. From a pioneer *Epilobium* association there develops one characterized by the genus *Raoulia*, plants remarkable for the development of strikingly unique cushion forms. Various species of these curious composites are abundant throughout the steppe formation, reaching their most striking development in the "vegetable sheep" association of certain rocky hillsides. The climax association of the river beds is a subalpine scrub of the usual type.—GEO. D. FULLER.

Iron bacteria.—A recent contribution by LIESKE[11] is of importance in that it supplements our knoweldge of the iron bacteria that has come to us largely through the writings of MOLISCH. It also revives interest in WINOGRADSKY's theory of iron assimilation, and illustrates in its comparative results the ever-present danger of generalizing from a too narrow inquiry into the field of research.

The author has made an intensive study of one of the numerous species of iron bacteria known as *Spirophyllum ferrugineum* Ellis, enlightening us regarding its specific cultural and physiological peculiarities. Unlike *Leptothrix octhracea* studied by MOLISCH, this bacterium does not grow in a medium containing organic matter; neither in an iron-free medium, nor in a medium containing iron salts other than ferrous carbonate or bicarbonate, nor salts of any of the other metals.

Of chief physiological importance is the experimental proof that the organism can utilize the carbon of CO_2 introduced into a flask from which every other source of carbon can be excluded; the nutrient medium contains in solution inorganic salts, iron filings are added, and CO_2 is furnished to the extent of 1 per cent of the air in the flask. Naturally, then, issue is taken with MOLISCH, who in his recent monograph (*Die Eisenbakterien*[12]) denies the correctness of WINOGRADSKY's hypothesis that iron bacteria require iron

[10] COCKAYNE, L., On the peopling by plants of the subalpine river bed of the Rakaia. Trans. and Proc. Bot. Soc. Edinburgh **24**[3]:104–125. 1911.

[11] LIESKE, R., Beiträge zur Kenntnis der Physiologie von *Spirophyllum ferrugineum* Ellis, einem typischen Eisenbakterium. Jahrb. Wiss. Bot. **49**:91–127. 1911.

[12] Reviewed in this journal, **50**:464.

for a source of energy and nutrition. The results of this investigation on *Spirophyllum ferrugineum* would make it appear that for certain of the iron bacteria the storage of iron is not brought about by mechanical means, as MOLISCH suggests.

Using PFEFFER's phrase "chemosynthesis," LIESKE draws attention to the fact that CO_2 is chemosynthetically assimilated by certain other species of oxidizing bacteria, such as WINOGRADSKY's nitrate and nitrite bacteria: those capable of transforming thiosulphates into tetrathionic and sulphuric acids; those splitting up H_2O_2; or those that are able to oxidize CH_4 and CO and utilizing the carbon contained therein directly. He then is of the opinion that this particular iron bacterium, *Spirophyllum ferrugineum*, acts in an entirely similar way, inasmuch as from an elementary analysis of organisms grown in a fluid medium containing inorganic salts, metallic iron, and no other source of C other than that supplied indirectly by the action of CO_2 on the metallic iron (forming ferrous carbonate), he was able to prove a distinct increase in the C content of the mass of bacterial filaments. LIESKE calculates that the quantity of ferric oxide that *Spirophyllum ferrugineum* must form from ferrous carbonate to gain one part of C is 750 parts, if roughly estimated in parallel to the requirements of the nitrite bacteria.

That this use of ferrous carbonate for the sole purpose of chemosynthesis of C applies to *all* iron bacteria is, as LIESKE states, questionable; but the fact that it now seems proved in the case of this particular iron bacterium lends new life to the hypothesis of WINOGRADSKY; and at the same time makes it necessary that new and more widespread study of the several species of iron bacteria be undertaken in a most thorough manner.—NORMAN MACL. HARRIS.

Forests of the Philippines.—A rather complete discussion of the economic aspect of the forests of the Philippines, based upon the investigations of WHITFORD, has been issued as a bulletin of the Bureau of Forestry of these Islands.[13] The first part deals with the classification of the various forest types, the importance of the diptocarp types being emphasized, the amount and quality of the lumber, the uses to which it is adapted, the character of the lumbering operations, and the forest products other than lumber. It includes the results of mechanical tests of 34 Philippine woods and a bibliography of both Spanish and English publications on the forestry of the islands. The second part is devoted to the description and illustration of over 100 of the principal tree species. The descriptions relate principally to the trunk, branch, leaf, and wood characters, and not to those of the reproductive parts.

[13] WHITFORD, H. N., The forests of the Philippines. P.I. Department of the Interior, Bureau of Forestry. Bull. no. 10. Part I, Forest types and products. pp. 94. *pls. 27*. Part II, The principal forest trees. pp. 113. *pls. 103*. Manila: Bureau of Printing. 1911.

The plates include photographic studies of the trunks and drawings of the leaves and fruit.

The forests dominated by members of the Dipterocarpaceae are by far the most important both in extent and in volume of merchantable timber. The composition of these forests is a simple one from the forester's or lumberman's standpoint, a given area seldom having more than 15 or 20 species of economic importance; and in the most productive of the dipterocarp forests, known as the lauan type, 95 per cent of the timber belongs to 6 dominant species. The same forest is complex from the standpoint of the botanist, since it contains 150–200 tree species, the greater number being too small to be economically important. Once within the tangled mass of lianas about the openings, these forests are easy to penetrate.

In addition to an abundance of timber for general construction purposes, these forests produce excellent substitutes for mahogany and lignum vitae, many valuable furniture woods, and woods suitable for carving, engraving, and numerous other purposes. Among the other forest products are resins, oils, rubber, rattan, and bamboo. Lumbering methods have been largely primitive, but these are being replaced by more scientific ones, which promise to produce not only all the timber required for use upon the islands, but considerable quantities for export.—GEO. D. FULLER.

African sand dunes.—The vegetation of a narrow border of sand dunes along the shores of the Bay of Algiers has been described by DUCELLIER.[14] An annual rainfall of over 60 cm., well distributed throughout the year, with a maximum in November and December, and a minimum in July and August, together with a mean temperature ranging from 5° C. in January to 30° C. in August, produces an evergreen vegetation with hardly a cessation of flowers throughout the year. Three distinct bands of vegetation correspond to three distinct topographic zones running parallel with the shore. First is the foredune, with a vegetation characterized by the abundance of annuals and grasses of the usual type, belonging to such well known genera as *Salsola*, *Cakile*, *Silene*, *Euphorbia*, and *Ammophila*. Within this comes a depression termed "bande humide," apparently the same as the "pannes" of European ecologists. Here the vegetation is a mixture of xerophytes, mesophytes, and such hydrophytic forms as species of *Juncus*, *Scirpus*, *Orchis*, *Typha*, and *Nerium*.

In the inland portion of the area there appear to be few dunes of any considerable size. The plants conspicuous in the fixation of the dunes are *Lotus creticus*, *Scabiosa rutaefolia*, and *Pistacia Lentiscus*, while the established dunes are occupied by *Olea europea*, *Pinus halepensis*, *Phillyrea media*, and a considerable number of shrubs and herbs mostly of decidedly xerophytic structure. Among the prominent families represented in the lists of species are the legumes

[14] DUCELLIER L., Étude phytogéographique des dunes de la Baie d'Alger. Rev. Gén. Bot. **23**:273–308; 321–339. 1911.

with 43 species, the composites with 42 species, the grasses with 55 species, the euphorbias with 7 species, and the orchids with 11 species.—GEO. D. FULLER.

Cuscuta and its host.—Investigating the relations existing between certain species of *Cuscuta* and various hosts, particularly with regard to the connection established between the phloem of parasite and that of the host, THODAY[15] concludes that the cell walls of the haustorial phloem degenerate, and are absorbed at the point of contact with the sieve plates of the host, and the naked protoplasm of the parasite applies itself to the sieve area of the host. No connecting threads of protoplasm are found, and the translocation of food substances appears to be by a passive filtration of the contents of the sieve tubes of the host, forced by internal pressure, escaping into the parasite. This and other evidence favors the conclusion that connecting threads of protoplasm occur only between genetically connected cells. The interpretation of the results contains glaring examples of teleology, as we are assured "that the parasite takes much trouble to make use of the host sieve fields as they are, and not to disturb the mechanics of the sieve tubes"!—GEO. D. FULLER.

The prairies.—Studying the prairies of Iowa, SHIMEK[16] concludes that they were originally covered with floras of six more or less distinct types, and gives lists of species for each. He reviews carefully the various theories as to the factors causing their development, and gives a rather extensive bibliography of the origin of this type of vegetation, with brief notes on many of the titles. His principal contribution consists in attempts to obtain quantitative determinations of certain of the factors which may have been efficient in causing prairie development. Conspicuous among the data obtained are those of the comparative rates of evaporation at prairie and forest stations of observation. These data, although very scanty, seem to be significant, and lead to the conculsion that "exposure to evaporation as determined by temperature, wind, and topography is the primary cause of the treelessness of the prairies."—GEO. D. FULLER.

---

[15] THODAY, MARY G. (SYKES), On the histological relations between *Cuscuta* and its host. Ann. Botany **35**: 655–682. 1911.

[16] SHIMEK, B., The prairies. State Univ. Iowa, Lab. Nat. Hist. Bull. **61**: 69–240. *pls. 13.* 1911.

60.

63.

GRIGGS on RHODOCHYTON

VOLUME LIII NUMBER 3

THE

BOTANICAL GAZETTE

MARCH 1912

THE MORPHOLOGY OF LEITNERIA FLORIDANA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 154

WANDA M. PFEIFFER

(WITH PLATES XVIII–XX)

Former investigators examining *Leitneria* have come to such different conclusions as to its proper place among Archichlamydeae that it seemed worth while to look into its morphology in the hope that some interesting situations might be uncovered.

Material and methods

The material used was obtained from plants in the Missouri Botanical Garden of St. Louis. The first material was collected during the winter and spring of 1908, and was killed in a dilute solution of chromo-acetic acid by Miss LAURA D. WATKINS, who sent it to the laboratory in 70 per cent alcohol. I spent the last week in March 1908 in St. Louis. Pollen of *Leitneria* was beginning to be shed on March 28, which gave me an opportunity to pollinate some of the flowers of pistillate plants which stood a considerable distance from any staminate ones. During this week I made frequent collections in the hope of obtaining fertilization stages.

In the next year, living material was sent to me about twice a week from early in January until late in July. I again spent the week when pollen was ripe in St. Louis, and pollinated practically all the pistillate catkins in the garden except those which grew on seven twigs which were covered with paper sacks in order to

prevent pollination. This last precaution was taken because the large amount of fruit produced in previous seasons on pistillate plants remote from staminate plants made the occurrence of parthenogenesis seem possible. The twigs bearing the catkins pollinated were carefully labeled, both as to the location in which they grew and the time of pollination. Again frequent collections (two every day) were made for about five days after pollination.

The first catkin collected had sections cut off each side to allow the more easy penetration of the killing fluid, and were then killed *in toto*. Owing to the difficulty in orienting the material, and to the fact that the hairs on the bracts made the cutting of smooth sections practically impossible, in all the later material the pistils and the stamens were picked out of the catkins before killing.

The young ovaries were killed in Flemming's weaker solution, while some of the later stages in the development of the ovule and of the seed were killed in 1 per cent chromo-acetic acid. The material was imbedded in paraffin and sections cut from 2–10 μ in thickness. The stains used were the combination of safranin and gentian violet, with the addition of gold orange in some cases. The solution of gold orange in clove oil to be used after clearing in clove oil was found to be more satisfactory than the alcoholic solution.

Historical

The work done on *Leitneria* previous to 1894 was largely taxonomic, and has been cited by TRELEASE (1) in a paper of that year describing the plants of *Leitneria* found growing in the lowlands of southeastern Missouri. He considered the habit and distribution of the plant and its various taxonomic features, and besides this the structure of the wood, calling attention to its extremely low specific gravity, and concluding with a discussion of the position *Leitneria* had held in various schemes of classification. The portion of the paper with which we are most concerned has to do with the catkins. Of these it is said:

On mature plants the upper axillary buds are generally flower buds, and develop in the autumn into oblong, erect, subsessile, hairy catkins, about half an inch long, surrounded at base by bud scales, which pass into the very acute scales of the inflorescence. The trees are dioecious. . . . . The flowers expand

before the leaves, early in March. . . . . The staminate catkins then become from one to two inches long, generally curved outward, and their scales spread just enough to expose the stamens and allow the very abundant and powdery yellow pollen to escape. The soft parenchyma of the axis of inflorescence becomes torn in various directions as the catkins elongate, so that when they have reached their full development it is loosely fissured throughout. . . . . The staminate flowers, so far as I have examined them, are glabrous and quite destitute of a perianth or involucre of any description, and consist simply of a whorl of about ten short filaments, a little dilated at base and surmounted by slightly versatile but nearly erect, extrorse, two-celled anthers, dehiscing longitudinally. The pollen grains are nearly globose, smooth, slightly 3-4-grooved with underlying thickening of the intine, and fall from the dehiscent anther very readily, and there is no doubt that the species is wind-pollinated.

The pistillate catkin possesses the same loose lacunose structure as the staminate, though the axis is far less torn. When fully developed they are rarely over half an inch long. . . . . Unlike the staminate flowers, the pistillate, which are limited to the upper axils, are very short-stalked or with a rudimentary disk, and possess a rudimentary involucre or perianth of a few small, glandular-fringed scales, the largest two of which stand nearly laterally, while the remainder are dispersed along the side next the axis of the catkin. Only one carpel is present. The ovary is shortly ovoid, finely pubescent, one-celled, and contains a single ascending parietal ovule with the micropyle directed upward. The green or slightly reddish style is attached a little at one side, and in anthesis curves outwards and becomes grooved on the stigmatic side, or somewhat flattened, with the stigmatic surface undulated, possessing the general characters of wind-pollinated stigmas. The placenta and stigmatic groove are turned away from the axis and face the bract, a very unusual position for the suture in a monocarpellary flower, and one which appears to indicate that the flower is in reality reduced from a former state in which there were two carpels radially arranged with reference to the bract, or perhaps a larger number. . . . .

The fruit is an erect drupe. . . . . Its surface is coarsely rugose reticulated over the firm fibrovascular bundles of the pericarp. Near the top it is marked by an oblique scar left by the caducous style, and it contains a single large seed with a straight embryo and rather thin layer of albumen.

The microsporangium

The microsporangium passes the winter in the mother cell stage. In the youngest stamen examined there were four microsporangia, each with a considerable amount of sporogenous tissue in the mother cell stage. The mother cells numbered as high as five across the sporangium, while beyond these there sometimes were

as many as six layers of cells, three of which might become tapetal, while the others formed the sporangium wall. On the opposite side of the sporangium the tapetum was usually only one layer of cells in thickness, these evidently derived from the sporogenous mass (fig. 1). In longitudinal section of the sporangium, the spore mother cells were seen to lie in plates somewhat separated from each other (fig. 1).

By the middle of February the separation of the plates of sporogenous cells from each other was marked (fig. 2). By this time the tapetal cells, especially those on the inner side of the sporangium, were beginning to break down and appeared as much distorted cells, while the tabular cells which formed the inner layers of the sporangium wall became very much flattened and took stain more readily (fig. 2).

In the mature anther the cell walls had all disappeared except the well-developed endothecium inside of the epidermis. There are two pollen sacs which dehisce longitudinally with no definite stomium.

The megasporangium

The earliest stage observed showed the megasporangium as a rather massive protuberance inward from the side wall of the ovary cavity. On January 21 some of the ovules showed the beginning of the inner integument. By February 16 the outer integument had begun its development, and the growth of the ovule had been such that a median longitudinal line through the ovule had been shifted from practically perpendicular to the longitudinal axis of the carpel to a position nearly parallel with it. The growth of the integuments from this time on was somewhat irregular, sometimes the outer and sometimes the inner growing more rapidly. There was in either case apparently an excessive development of integuments, so that when the embryo sac was ready for fertilization they not only closed over the nucellus, but lay in folds above it (fig. 3). At this stage the innermost layer of cells of the inner integument had much greater cytoplasmic contents than the other cells.

In the nucellus, which was relatively massive, there was evidently one archesporial cell picked out. The earliest stage examined

showed a single sporogenous cell and two parietal cells (fig. 4), which evidently arose by the periclinal division of the primary parietal cell. The further division of the parietal cells continued steadily, so that within four weeks there were often more than 10 parietal cells lying between the sporogenous cell and the epidermis (fig. 5). Very often a periclinal division of the epidermal cells of the nucellus occurred (fig. 5). The time when the mother cell went into synapsis varied greatly, some of the ovules showing this condition as early as February 16 (fig. 5), while others showed the mother cell in a presynaptic condition as late as March 22. However, at this later date the majority of mother cells were in synapsis.

Although the division of the megaspore mother cell was not observed, it evidently gave rise to a linear tetrad of megaspores. Above the micropylar end of the young embryo sac there were often three deeply stained masses (fig. 6), which had the same appearance as recognized abortive megaspores in other forms.

As the embryo sac developed, the further periclinal and anticlinal divisions of the parietal tissue continued, so that when the sac was ready for fertilization there were often as many as 30 layers of cells lying above it. Very often the tip of the nucellus developed into a somewhat slender beak, which took the form of the more or less twisted integuments (fig. 3).

The female gametophyte

After the formation of the row of megaspores, the innermost or functional spore immediately began division. In material collected on March 21 and killed on March 25 the embryo sacs were practically all in the four-celled stage. The two-celled stage figured (fig. 6) was of material killed on March 25 of the preceding year. It would seem that the embryo sac remained in the four-celled stage for some time, since material killed on March 30, April 3, and April 5 showed practically all the sacs in this condition. An ovule killed in the afternoon of April 5 showed the simultaneous division of these four nuclei to form the light nuclei of the completed sac.

In the mature embryo sac the egg has the usual organization, with the vacuole toward the micropylar end, but the synergids

are almost entirely without vacuoles and the position of their nuclei is irregular (fig. 7). The antipodals are usually evanescent.

The male gametophyte

The stages of pollen tube formation and of fertilization were not observed, and this fact, under ordinary circumstances, might have led to the belief that the form was parthenogenetic. This makes peculiarly fortunate the precaution which was taken early in the season, of preventing pollination in some of the pistillate catkins. As has been described previously, this was accomplished by covering with paper sacks seven of the twigs bearing pistillate flowers before pollen began to fly. Although each of these twigs bore about five catkins and each catkin contained several pistils, there was not a single case of seed formation observed. One may safely infer that parthenogenesis is not of usual occurrence in this form.

The endosperm

The fusion of the polar nuclei and male cell was not observed, but must have occurred about April 15. Material killed on this date showed the eight-nucleate sac, but material killed on April 16 showed the large endosperm nucleus. It may be that division of this nucleus did not take place immediately, since all the material examined within the five days following this shows it undivided. Material killed on April 22 showed two free endosperm nuclei. After this, the simultaneous free nuclear division goes on rapidly, so that by the time the division of the fertilized egg occurred there were sometimes as many as 35 of these parietally placed nuclei to be seen in a single section (fig. 8*a*). The increase in size of the sac, due to growth of the ovule itself, and the breaking down of tissues about the sac and especially below it was very great. By May 10 the endosperm was seen as a very thin layer of cytoplasm about the embryo sac, which extended over three-quarters of the length of the ovule, which itself measured as much as 6 mm. About this time the formation of walls in the endosperm began, and this was followed by a centripetal growth of tissue so regular as to give the endosperm the appearance of being made up of plates of cells. These cells were large and contained unusually large nuclei. This

was especially true of the tissue at the chalazal end, which was a very loose tissue and contained large, irregular nuclei, which were possibly produced by the fusion of several nuclei.

The embryo

After free nuclear division had continued for some time in the endosperm, the division of the fertilized egg occurred. The first two-celled embryos seen were in material which was killed April 30. It was a matter of indifference in which plane the first division wall should lie, so that in some cases (fig. 8) the first wall was parallel to the longitudinal axis of the embryo sac, while in others the position was the horizontal one almost universal in the embryos of angiosperms. In whichever plane the first division occurred, other divisions followed rapidly in all planes, so that there was in no case a slender suspensor formed. In fact, in the young stages the embryo was somewhat pear-shaped, with the massive suspensor only slightly narrower than the body of the embryo (fig. 9*a*).

The growth of the embryo, and indeed of the whole fruit, was very rapid. Figs. 8*a*, 9*a*, and 10*a*, which were drawn to the same scale, show the increase in size of the embryo itself within the first five weeks. Fig. 9 shows the detail of a few cells of the endosperm and the outermost layer of cells of the embryo at the micropylar end of the embryo sac. It will be noticed that at this stage, when the embryo consisted of a relatively large number of cells, there was as yet no evidence of the appearance of cotyledons (fig. 9*a*), the embryo proper still appearing as a globular mass of cells. Shortly after this, however, the cotyledons began to appear as protuberances from the distal end of the embryo, and within a few weeks there was the well-organized embryo as shown in the diagram (fig. 10*a*.) Cell detail of the suspensor region of the embryo is shown in fig. 10, where it will be noticed in comparison with fig. 9, which shows some of the outer cells of this region, that there had been but slight increase in the size of the cells of this region. Fig. 11 shows, under slightly less magnification than fig. 10, the detail of cell structure of the root end of the embryo and the lower portion of the suspensor. At this stage, examination even under low magnification showed a clearly defined periblem (fig. 10*a*). Under

higher magnification (fig. 11) it was seen that plerome, dermatogen, and calyptrogen all arose from a common group of meristematic cells, and that these regions were not yet clearly defined. The periblem was more easily picked out by the larger size of its cells and their relatively less cytoplasmic contents. At this stage of the embryo it was evident that the cotyledons were to be net-veined, as might be expected. The rapid growth of the embryo continued until at maturity it approached 1 dm. in length. Fig. 12 is a diagram showing the size of the seed and the position of the embryo within it.

The seed

The tremendous rate of growth of the seed made it seem worth while to look somewhat into the method of food supply. In the development of the ovule there was a very early differentiation of tissue in the chalaza. On March 25, when the embryo sac was in the two-nucleate stage, there was seen extending across the chalaza, from the base of the inner integument, a rather narrow layer of cells, which, having more densely granular cytoplasmic content, took a deeper stain than the other cells of the region (fig. 14). Immediately outside of this layer of cells, which for convenience we will speak of as the nutritive layer, there was a layer of cells elongated transversely to the axis of the ovule, which was continuous with the vascular bundle of the funiculus (figs. 13 and 14).

The cells of the nutritive layer divided repeatedly, so that by the time the development of the embryo sac was completed there was quite a mass of them showing very clearly, even under low magnification, on account of their deeper stain. At about the time that the embryo sac was ready for fertilization, the appearance of these cells changed, and under low magnification they could now be picked out by their lighter stain. Higher magnification showed them to have almost no granular cytoplasmic content (fig. 15). Very shortly after this it was seen that there was being deposited in the cells some reserve material, probably tannin, which did not stain with the iron-haemotoxylin combination. This deposition began at the periphery of the cell and proceeded toward the

interior (fig. 16). Finally the cells were so packed with material that it was impossible to distinguish even the nuclei.

As the endosperm nuclei began division, growth in all parts of the ovule became very rapid, and this rapid rate of growth continued up to the maturity of the seed. While this was going on the reserve material in the nutritive layer began to disappear gradually, and as it went the cells of the perisperm immediately above it, which had increased considerably in size, were seen to contain numbers of starch grains (fig. 17).

Coincident with the differentiation of the nutritive cells is the development of the conducting cells immediately below it. Fig. 14 shows the elongation of the cells of this region, and their general relation to the nutritive layer when it could first be distinguished in the condition of the ovule seen in fig. 13. Somewhat later the thickening of the walls of these elongated cells to form tracheary tissue was seen (fig. 18). At the time when the nutritive layer is most conspicuous on account of its large amount of reserve material, a section tangential to the disk of nutritive cells immediately below it shows the conducting tissue in the form of a radiating plate of tracheary tissue (fig. 19), so that very often in the longitudinal section through the ovule there were found transverse and oblique sections of the vessels rather than longitudinal as seen in fig. 17.

At maturity the seed consisted of an embryo with two thin, very broad cotyledons. About the embryo was a considerable mass of large-celled endosperm tissue whose cells were packed with starch. The perisperm was a relatively thin layer of loose tissue. These regions, as well as the relative thickness of the seed coats, are seen in the diagram (fig. 12). Immediately outside of the epidermal layer of the nucellus there is a thick layer of cutin, which entirely covers the micropylar end of the seed. So closely abutting this layer of cutin that it is impossible to tell whether it was laid down by these epidermal cells of the nucellus or by the innermost layer of cells of the integument, lies the inner integument. It seems probable that the cells of both these closely abutting layers may have contributed to the layer of cutin lying between them. These cells of the innermost layer are the only cells of the inner integuments which are at all conspicuous. In these cells the walls

had become irregularly thickened, so as to have a pitted appearance in surface view. The outer layers of cells of this integument have all collapsed, as is best seen in fig. 20. In the outer integument the development had been different, for while here too the outermost layer of cells had unthickened walls, all the remaining cells had the pitted wall (fig. 20), giving in section a rather conspicuous seed coat. It is interesting to note that the outer integument, which in the early stages of the development of the ovule seemed excessively developed (fig. 7), here extended but a very little distance beyond the tip of the nucellus (fig. 12).

Discussion

In handling a form about whose position taxonomically there have been so many differences of opinion, it seems worth while to attempt to summarize the forms which are similar to *Leitneria* in various particulars, in order to see whether it could be placed on the basis of its morphology.

In the case of the stamen, there is no particular in which it differs strikingly from the stamen of other catkin-bearing forms. The microsporangia pass the winter in the spore mother cell stage, as do those of *Salix glaucophylla* (2), *Alnus glutinosa* (3), *Corylus americana* (3), and *Ulmus americana* (4). That such a character should be given little weight taxonomically, however, becomes evident when one looks at such a group as Hamamelidaceae. SHOEMAKER (5) in his study of this family reports all variations in the stage in which the stamens of the different genera of spring-flowering forms pass the winter. Of *Liquidambar Styraciflua* he says "stamens are only small protuberances which do not show any archesporium"; of *Fothergilla Gardeni*, "they pass the winter in the pollen mother cell stage"; while of *Hamamelis arborea* and *Corylopsis pauciflora*, the stamens "pass the winter containing nearly mature pollen grains with two free nuclei."

The developing megasporangium containing a single archesporial cell differs from most of the Amentiferae yet reported upon. However, this condition is found in *Betula alba* (6) and in *Alnus glutinosa* (6), and is usual in various species of *Salix* (2), and therefore the character of a multicellular archesporium could hardly be

considered a group character. Again, the extent of tissue development in the nucellar region is so variable a character that one finds reports of deeply placed embryo sacs, such as are found in *Leitneria*, reported in *Casuarina* (**7, 8**), in *Triticum* (**9**), in *Cuphaea* (**10**), and in other entirely unrelated forms.

Another character which *Leitneria* has in common with the majority of Archichlamydeae is the initiation of the development of the embryo sac by a megaspore rather than by a megaspore mother cell, so that while a tetrad of spores is formed, a single megaspore functions. In the embryo sac that develops from this megaspore the synergids are characterized by being full of cytoplasm, rather than by having the large, distinct vacuole, as often found in the antipodal end of the cell. This, while a character not often reported for the synergids of forms even where the synergids are relatively small, is of course not a character which would hold any weight taxonomically. The ephemeral antipodals are found in many forms, as in the Salicaceae and Cupuliferae.

After fertilization, the behavior of the endosperm nucleus and of the fertilized egg is in no way extraordinary; while extreme in some cases, as in the great development of free nuclei of the endosperm before the division of the fertilized egg occurs, still there is no character of first importance which would indicate relationship with one family or another. Thus the more or less extensive development of free endosperm nuclei before the segmentation of the egg is a character shared by *Piper* (**11**) and *Asclepias* (**12**). The very regular centripetal growth of endosperm tissue after walls appear is extreme, and is rarely found so well developed in angiospermous seeds. The most striking character of the embryo itself is the massive suspensor. But this character, too, is shared by most of those forms, such a *Peperomia pellucida* (**13**), in which the first division of the fertilized egg may be longitudinal rather than transverse. It is of interest to find here again a form in which there is no fixed sequence of cell divisions in the development of the embryo, such as have long been emphasized in such forms as *Capsella*.

One might go on indefinitely pointing out some particular in which *Leitneria* resembles one or the other of the Archichlamydeae,

without in the end establishing any definite relationship with a specific group. The thing which does impress one, however, in looking over the work that has been done on Amentiferae, is the general resemblance to gymnosperms. Thus in working through the life history of such a form as *Leitneria*, one is constantly reminded of gymnosperms by one detail of structure or another. Thus, in the wood of *Leitneria*, one finds tracheae which show in every case an incomplete disappearance of the cross walls of the rather short cells of which they are composed, so that in section one sees clearly at the periphery of the vessel the remains of these walls. More striking than this incomplete disappearance of septa across the tracheae is the predominance of tracheids with bordered pits.

As might be expected, it is in the study of the reproductive parts that one finds the most striking reminders of gymnosperm structure. Thus it is a relatively easy matter to imagine the derivation of a catkin from the compound strobilus found among gymnosperms. In either case the structure is made up of a series of bracts in whose axil stand sporophylls. In both gymnosperms and the Amentiferae the characteristic number of megasporophylls per bract is two, but it is in no way surprising to find this number occasionally reduced to one, as in *Leitneria*, while in the larger number of miscrosporophylls per bract we have a parallel among Gnetales, the only group of gymnosperms which has the compound staminate strobilus.

Within the carpel the ovule also has several characters in which it resembles that of gymnosperms. Thus we find that it is a relatively massive structure, with a large development of nucellar tissue above the megaspore, so that the female gametophyte when it develops is deeply placed in tissue.

Summary

The microsporangium passes the winter in the spore mother cell stage.

In the solitary ovule, the archesporial cell divides early; on January 21 there were two parietal cells above the single archesporial cell.

There is a large development of parietal tissue in the ovule, as many as thirty layers of cells lying above the embryo sac at its maturity.

Practically all megaspore mother cells were in synapsis on March 22.

A linear tetrad of megaspores was evidently formed.

By April 7 practically all embryo sacs showed the eight-nucleate female gametophyte.

After fertilization the endosperm nucleus divides repeatedly, giving rise to a large number of free nuclei before the division of the fertilized egg occurs.

After wall formation in the endosperm begins, there is an extremely regular centripetal growth of tissue.

The first division of the fertilized egg may be longitudinal or transverse; in either case a massive suspensor is formed.

The young embryo is a pear-shaped mass which is composed of hundreds of cells before the cotyledons appear.

In the root tip of the embryo, calyptrogen, dermatogen, and plerome arise from a common meristematic group of cells.

The growth of the seed is very rapid, and at maturity it contains a large, flat, dicotyledonous embryo, a thin layer of endosperm tissue, and a few layers of perisperm cells.

The seed coat is formed mostly from the outer integument, the inner integument contributing only its innermost layer of cells.

The morphology of *Leitneria* is not such as would make it possible to place it definitely in any of the families of the Archichlamydeae, but, in common with other Amentiferae, it suggests the possibility of the derivation of Amentiferae from such forms as one finds among the gymnosperms which have compound strobili.

The author is indebted to Professors John M. Coulter and Charles J. Chamberlain, under whose direction this work was done, and to the staff of the Missouri Botanical Garden of St. Louis for aid in collecting material.

The University of Chicago

LITERATURE CITED

1. TRELEASE, WILLIAM, *Leitneria floridana*. Rept. Mo. Bot. Garden **6**: 1–26. *pls. 30–44.* 1895.
2. CHAMBERLAIN, CHARLES J., Contributions to the life history of *Salix*. BOT. GAZ. **23**: 147–179. *pls. 12–18.* 1897.
3. ———, Winter conditions of certain sporangia. BOT. GAZ. **25**: 124–128. *pl. 11.* 1898.
4. SHATTUCK, CHARLES H., A morphological study of *Ulmus americana*. BOT. GAZ. **40**: 209–223. *pls. 7–9.* 1905.
5. SHOEMAKER, D. N., On the development of *Hamamelis virginiana*. BOT. GAZ. **39**: 248–266. *pls. 6, 7.* 1905.
6. BENSON, MARGARET, Contributions to the embryology of the Amentiferae. I. Trans. Linn. Soc. London **3**: 409–424. *pls. 67–72.* 1894.
7. TREUB, M., Sur les Casuarinées et leur place dans le système naturel. Ann. Jard. Bot. Buitenzorg **10**: 145–231. *pls. 12–32.* 1891.
8. FRYE, T. C., The embryo sac of *Casuarina stricta*. BOT. GAZ. **36**: 101–113. *pl. 17.* 1903.
9. KOERNICKE, M., Untersuchungen über die Entstehung und Entwickelung der Sexualorgane von *Triticum* mit besonderer Berücksichtigung der Kerntheilung. Verhandl. Natur. Hist. Ver Preussen Rheinl. **53**: 149–185. 1896.
10. GUIGNARD, L., Recherches sur le sac embryonnaire des Phanérogames Angiospermes. Ann. Sci. Nat. Bot. VI. **13**: 136–199. *pls. 3–7.* 1882.
11. JOHNSON, D. S., On the development of certain Piperaceae. BOT. GAZ. **34**: 321–340. *pls. 9, 10.* 1902.
12. FRYE, T. C., A morphological study of certain Asclepiadaceae. BOT. GAZ. **34**: 389–413. *pls. 13–15.* 1902.
13. JOHNSON, D. S., On the endosperm and embryo of *Peperomia pellucida*. BOT. GAZ. **30**: 1–11. *pl. 1.* 1900.

EXPLANATION OF PLATES XVIII–XX

All figures were made with an Abbé camera lucida. A Zeiss microscope was used with ocular 4 and objectives 2/3 and 2 mm.

Abbreviations: *a*, antipodals; *en*, endosperm; *em*, embryo; *n*, nutritive layer; *c*, conducting tissue; *o*, outer integument; *i*, inner integument.

FIG. 1.—Portion of a longitudinal section of a stamen in winter condition; ×600.

FIG. 2.—Similar portion of a stamen Feb. 16, showing the separation of the plates of spore mother cells and the breaking down of tapetal cells; ×600.

FIG. 3.—A diagram through the ovule when the embryo sac is mature, showing the position of the embryo sac and the great development of integuments; ×600.

PFEIFFER on LEITNERIA

PFEIFFER 'RIA

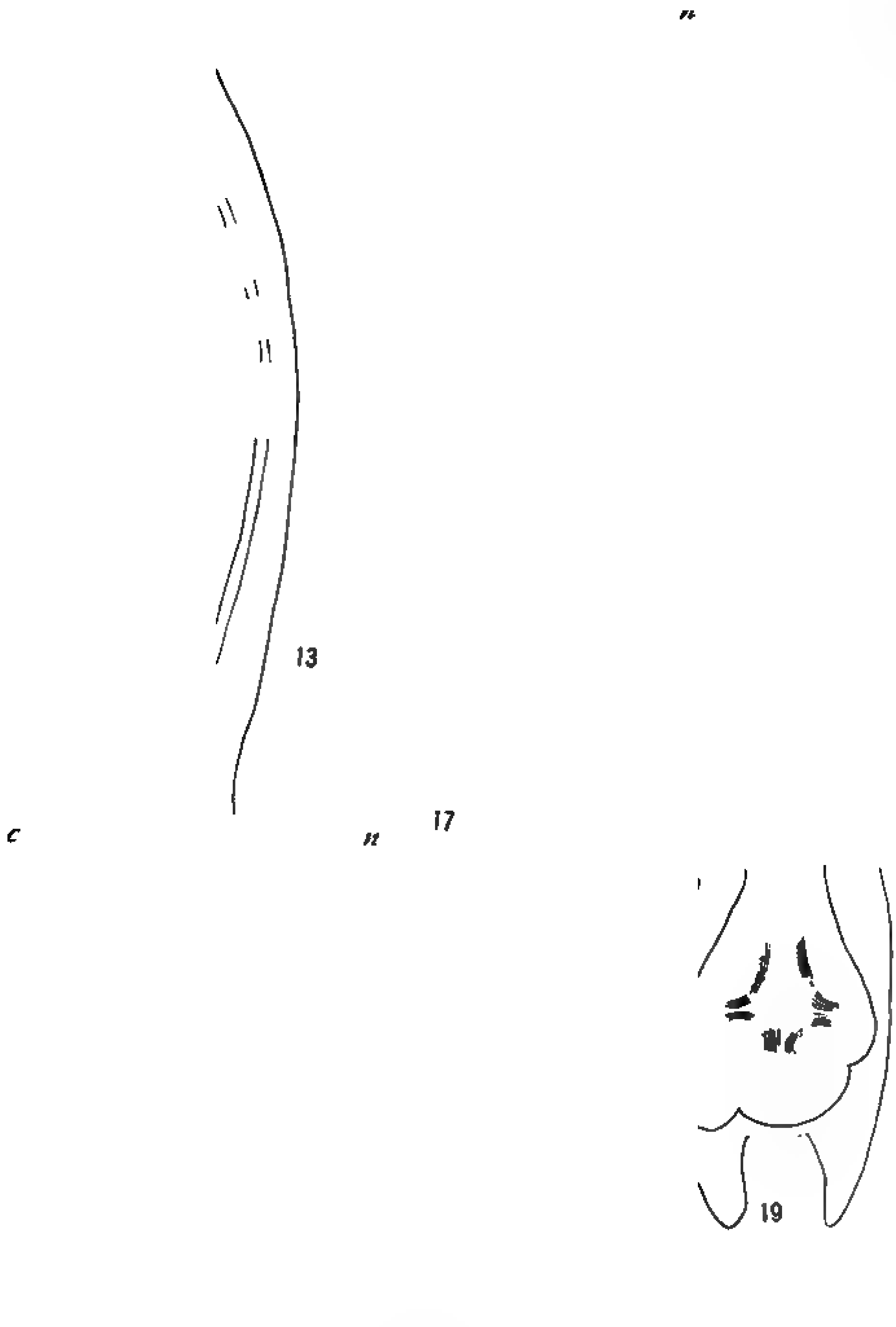

n
13
c
n
17
19

FIG. 4.—Portion of [illegible]
nous cell and two parietal [illegible]

FIG. 5.—Portion [illegible]
sion of some of the epidermal [illegible]
and the megaspore mother [illegible]

FIG. 6.—Two-nucleate [illegible]
spores immediately above [illegible]

FIG. 7.—The egg [illegible]

FIG. 8.—Two-celled [illegible]
fertilized egg. × 500.

FIG. 8a.—Diagram showing [illegible]
fig. 8, and the extensive [illegible]

FIG. 9.—Detail [illegible]
at *d* in fig. 9a and the [illegible]

FIG. 9a.—Diagram showing [illegible]
of a slender suspensor [illegible]

FIG. 10.—Detail [illegible]
in fig. 10a; × 500.

FIG. 10a.—Diagram [illegible]
dons; × 55.

FIG. 11.—Detail [illegible]
lower portion of the [illegible]

FIG. 12.—Diagram [illegible]
and the extent of the [illegible]

FIG. 13.—Diagram [illegible]
tive layer showing [illegible]
marked out [illegible]

FIG. 14.—Detail [illegible]
13, showing the [illegible]
and the [illegible]
tinguished [illegible]

FIG. [illegible]
almost free [illegible]

FIG. [illegible]
has begun [illegible]

FIG. [illegible]
layer again [illegible]

FIG. [illegible]
tion [illegible]

FIG. [illegible]
[illegible]

FIG. [illegible]

THE INFLUENCE OF THE SEED UPON THE SIZE OF THE FRUIT IN STAPHYLEA. I

J. Arthur Harris

(WITH FOUR FIGURES)

A previous paper in this journal[1] reviewed the chief literature bearing on the theory that the size attained by a fruit is to some extent determined by a stimulus exerted by the developing seed. The purpose of the present contribution is to consider the data from two series comprising 3277 fruits of *Staphylea*, collected in a manner to permit of carrying the analysis somewhat farther than was possible with the *Cercis* material.

I. Nature of the characters considered

The fruit of *Staphylea trifolia* is familiar to botanists as a three-lobed, three-celled, membranaçeous, inflated pod, producing from 0 to 4 bony seeds in each locule. Unfortunately it is hardly of the form one would select especially for an investigation of the size. Its considerable irregularity renders measurement difficult, and its lightness makes weighing tedious. Its use in the present study is in part a consequence of the ease with which the necessary data could be obtained in connection with other studies of fertility and fecundity in the species, and in part a result of special advantages which will be apparent to the reader later.

In a fruit whose shape and texture precludes any very accurate determination of size, the thing to be done is to take measurements on a scale coarse enough that minor irregularities will not be of much account. Having done this, we should not attach great importance to the exact values of the calculated constants, but look at them as merely rough approximations. Consistent results from a number of individual series will strengthen our confidence in the soundness of our conclusions, but if the relationships are of a very slight intensity, we should expect, for reasons well known

[1] Harris, J. Arthur, On the relationship between the length of the pod and fertility and fecundity in *Cercis*. Bot. Gaz. 50:117–127. 1910.

to the statistician, different series of material to yield somewhat discordant results.

For a first study it seemed undesirable, considering the irregularity of the pod, to take measurements in fine units, and readings were made of the length of the fruit to the nearest 0.5 cm. The number of ovules formed and the number of seeds developing can be fairly easily counted.

II. Material

Shrubs of *Staphylea* growing in the "North American Tract" of the Missouri Botanical Garden furnished the material for this investigation. These are in part the individuals upon which a study of selective elimination[2] was based in the spring of 1908, and the numbers of the plants are comparable.

In 1906 the fruiting of *Staphylea* seemed to be quite normal, and a series of about 100 fruits each were obtained from 20 shrubs. In 1907 there was a severe frost which inhibited entirely the fruiting of some of the trees; altogether only 1218 fruits were obtained, as compared with 2059 in 1906. In 1906 the fruits were taken from shrubs 11–20, but in 1907 it was necessary to take shrubs 11–41 to get 16 individual series of material of suitable size. Only three-loculed fruits were used.

In the reduction of the data the biometric methods, now familiar in a general way to most working biologists, were used.[3] For the benefit of biologists who are inclined to be wary of mathematical symbols, I may explain that no difficulties of that kind will be met if a few simple ideas are kept in mind. For convenience and terseness of expression, the characters investigated are designated by letters: o = number of ovules per locule[4]; s = number of seeds per locule[4]; f = number of ovules failing to develop to mature seeds per locule[4]; p = position of fruit on the inflorescence; n = number of fruits per inflorescence; $r_{ls} > r_{lo}$ is to be read "the correlation (r being the symbol for correlation) between the length of the pod

[2] HARRIS, J. ARTHUR, On the selective elimination occurring during the development of the fruit of *Staphylea*. Biometrika 7:452–504. 1910.

[3] Unless especially noted, SHEPPARD's correction was not used for the second moment.

[4] Or occasionally total number per fruit, when this is indicated by the context.

and the number of seeds developing is greater than the correlation between the length of the fruit and the number of ovules formed."

III. Analysis of data

We first examine our data to ascertain whether there is a measurable degree of interdependence between the length of fruit and the number of ovules formed, and between the length of fruit and the number of seeds developing per locule.

A. DISCUSSION OF DATA FROM INDIVIDUAL SHRUBS

Perhaps the criticism, in these days, most generally directed at biometric work is that in the massing of large numbers of individuals into correlation tables, biological relationships which otherwise might be recognized are obscured. "The fundamental requisite for the validity of biometric constants is the homogeneity of the material upon which they are based," we are told. There is more than one word to be said on this point, but certainly it is always desirable to consider data in as minutely analyzed form as can be done without incurring too great dangers incident to the probable errors of random sampling.

From PEARSON's investigations[5] we know that plant individuals of the same race are somewhat differentiated among themselves with respect to the characters of the organs which they produce. In short, they are *individual* really as well as nominally. The combination of series of fruits taken from a small number of plants might influence to some extent the correlation constants describing the relationship between the fertility of the fruit and its length. To free our results as far as possible from any such source of error, I first consider the relationship of the number of ovules formed (o) and the number of seeds developing (s) to the length of the fruit (l) in each of the 20 shrubs of the 1906 series, and each of the 16 of the 1907 collection. In the large series it is also of interest to compare the correlation for the length of fruit and number of ovules failing to develop into mature seeds (f). For these relationships 92 correlation tables are necessary. While experience has shown that it is desirable that all tables of data should be published, it really

[5] PEARSON, K., and others. Phil. Trans. Roy. Soc. London A **197**:285–379. 1901.

seems unreasonable to ask a publisher to print such a series. I retain my original tables, which are available to anyone desiring to consult them, and have deposited a duplicate set in the Library of the Missouri Botanical Garden.

TABLE I

CORRELATIONS FOR FRUIT LENGTH AND FERTILITY; 1906 SERIES

Number of shrub	r_{lo}, Length and ovules per locule	r/E_r	r_{ls}, Length and seeds per locule	r/E_r	r_{lf}, Length and ovules failing per locule	r/E_r
11........	$-.246\pm.035$	7.02	$.376\pm.032$	11.75	$-.399\pm.031$	12.87
12........	$.201\pm.034$	5.91	$.347\pm.031$	11.18	$-.093\pm.035$	2.66
13........	$.300\pm.035$	8.56	$.537\pm.027$	19.87	$-.258\pm.036$	7.17
14........	$.103\pm.039$	2.63	$.328\pm.035$	9.36	$-.185\pm.038$	4.87
15........	$.124\pm.037$	3.34	$.247\pm.035$	7.05	$-.042\pm.038$	1.08
16........	$.180\pm.038$	4.74	$.347\pm.034$	10.19	$-.083\pm.039$	2.13
17........	$.198\pm.037$	5.35	$.311\pm.035$	8.87	$-.050\pm.038$	1.30
18........	$.014\pm.039$	.36	$.343\pm.034$	10.07	$-.264\pm.036$	7.30
19........	$.068\pm.039$	1.75	$.320\pm.035$	9.14	$-.129\pm.038$	3.32
20........	$.117\pm.037$	3.15	$.533\pm.027$	19.75	$-.325\pm.033$	9.84
21........	$.026\pm.039$	.67	$.439\pm.031$	14.15	$-.382\pm.034$	11.22
22........	$.333\pm.034$	9.78	$.343\pm.034$	10.10	$-.166\pm.037$	4.48
23........	$.096\pm.039$	2.44	$.315\pm.035$	8.98	$-.153\pm.039$	3.91
24........	$.244\pm.037$	6.58	$.418\pm.032$	13.05	$-.178\pm.038$	4.67
25........	$.175\pm.038$	4.59	$.475\pm.030$	15.83	$-.300\pm.035$	8.56
26........	$.167\pm.038$	4.40	$.456\pm.031$	14.70	$-.225\pm.037$	6.08
27........	$.247\pm.037$	6.68	$.421\pm.032$	13.15	$-.139\pm.038$	3.67
28........	$.082\pm.038$	2.14	$.364\pm.033$	11.02	$-.227\pm.036$	6.31
29........	$.093\pm.039$	2.37	$.415\pm.032$	12.95	$-.270\pm.036$	7.50
30........	$.043\pm.039$	1.08	$.402\pm.033$	12.18	$-.297\pm.036$	8.25

The physical constants (means, standard deviations, and coefficients of variation) for the characters dealt with need not detain us here. The correlations for the 1906 series are given in table I, and for the 1907 series in table II.[6] Assuming, as is generally done, that a correlation coefficient of 2.5 times its probable error may be regarded significant, we may examine the results for the 1906 series.

In one case r_{lo} is significantly negative; the remaining 19 constants are all positive, and 12 are greater than 2.5 E_r. There can be no doubt of the significantly positive correlation between length and number of seeds per locule. Comparing r_{lo} and r_{ls} by means of

[6] In calculating the probable errors for these individuals, N was taken as the number of locules, not as the actual number of fruits; perhaps the latter course would have been better. There is always some question as to what should be done in cases of this kind. See PEARSON, Phil. Trans. Roy. Soc. A **197**:295, footnote; HARRIS, Biometrika **7**:308–309. 1910.

TABLE II

CORRELATIONS FOR FRUIT LENGTH AND FERTILITY; 1907 SERIES

Number of shrub	r_{lo}, Length and ovules per locule	r/E_r	r_{ls}, Length and seeds per locule	r/E_r
11	.261±.057	4.56	.296±.056	5.26
17	.383±.046	8.41	.148±.052	2.84
19	−.005±.047	.11	.271±.043	6.28
24	.101±.038	2.64	.291±.035	8.24
29	.154±.046	3.36	.424±.039	10.96
31	.132±.038	3.53	.421±.031	13.42
32	.135±.043	3.14	.305±.040	7.67
33	.152±.039	3.88	.397±.034	11.75
34	.168±.043	3.95	.490±.033	14.72
35	−.022±.046	.48	.439±.037	11.94
36	.376±.043	8.79	.467±.039	11.98
37	.021±.040	.53	.419±.033	12.78
38	.040±.040	.99	.398±.034	11.84
39	.209±.057	3.65	.413±.050	8.32
40	−.255±.036	7.05	.334±.034	9.71
41	.132±.049	2.70	.303±.045	6.69

table III, we find in every case $r_{ls} > r_{lo}$, and that in 17 cases of the 20 it is significantly greater in comparison with its probable error. All the correlations for l and f are negative, and 17 out of the 20 may be safely regarded as significantly negative.

TABLE III

$r_{ls}-r_{lo}$ FOR 1906

Number of shrub	Difference $r_{ls}-r_{lo}$	Difference / P.E. diff.
11	.622±.047	13.23
12	.146±.046	3.17
13	.237±.044	5.38
14	.225±.052	4.33
15	.123±.051	2.41
16	.166±.051	3.26
17	.112±.051	2.20
18	.329±.052	6.32
19	.252±.052	4.84
20	.417±.046	9.06
21	.413±.050	8.25
22	.011±.048	.22
23	.219±.052	4.21
24	.174±.049	3.56
25	.300±.048	6.26
26	.288±.049	5.89
27	.173±.049	3.54
28	.282±.050	5.65
29	.322±.050	6.44
30	.360±.051	7.05

TABLE IV

$r_{ls}-r_{lo}$ FOR 1907

Number of shrub	Difference $r_{ls}-r_{lo}$	Difference / P.E. diff.
11	.034±.080	.43
17	−.235±.069	3.39
19	.276±.063	4.35
24	.190±.052	3.65
29	.270±.060	4.50
31	.289±.049	5.91
32	.169±.059	2.90
33	.245±.052	4.73
34	.322±.054	5.95
35	.461±.059	7.88
36	.091±.058	1.58
37	.398±.052	7.73
38	.358±.052	6.86
39	.204±.076	2.70
40	.589±.050	11.79
41	.171±.067	2.57

For the 16 plants of the 1907 series, the correlation for length and ovules is positive in 13 cases, and negative in 3; significantly negative in one instance, and significantly positive in 11. The values are low, but, as in 1906, there seems to be a slight positive relationship between the length of the pod and the number of ovules formed.

For length and number of seeds all the correlations are positive, and all are significantly positive with regard to their probable errors. Furthermore, they are of a substantial order of magnitude, ranging from 0.150 to 0.500.

Comparing, as in 1906, by taking the differences $r_{ls}-r_{lo}$, with their probable errors as shown in table IV, we find that in one case the difference is negative[7]; of the 15 positive differences, 13 are over 2.5 times their probable error and hence trustworthy.

Diagrams for r_{lo}, r_{ls}, and $r_{ls}-r_{lo}$ make the relationship very clear. Graphs for only one year (1906) need be published. In these diagrams (fig. 1) the vertical line represents the zero line on either side of which the constants would fail if they were due merely to the chance errors of random sampling. The magnitude of the constants for the individuals, or the difference in their correlations, is shown by the length, and the sign by the direction of the bars. The amount of the constant which might be due to the probable errors of random sampling (2.5 times its probable error) is shown by the unshaded area, while the shaded portion gives some idea of the biological trustworthiness of the constant. These diagrams make very clear to the eye that

1. The length of the fruit and both the number of ovules formed and the number of seeds developing are interdependent, and often moderately closely interdependent.

2. The correlation for length and number of seeds per locule is significantly higher than that for length and number of ovules per locule.

3. These two facts taken in conjunction indicate that there is some physiological relationship between the length of the fruit and the number of seeds developing.

[7] It is significantly negative in comparison with its probable error. I find no slip in the arithmetic. The constant is based on only 53 pods, and so too much significance must not be attached to it.

B. DISCUSSION OF DATA FROM GENERAL SAMPLES

In the foregoing section, samples from each tree were treated individually, because heterogeneity of material may have a considerable influence upon correlation. The constant for any single individual cannot be taken to typify *Staphylea trifolia* as a species. Not only is each plant in some measure individual, but the constants based upon a small series of fruits may be too large or too

FIG. 1.—Diagram to show intensity of correlation between ovules and length (r_{lo}), seeds and length (r_{ls}), and their difference ($r_{lo}-r_{ls}$), in 20 individuals of *Staphylea;* the individuals are numbered 11 to 30 from the top of the diagram; the length of the bars shows the intensity of the correlation, and the shaded area the statistically significant amount, that is, the excess over 2.5 times the probable error.

small by an amount known as the probable error of random sampling.

To free our constants as far as possible from the influence of probable errors, and to gain more definite conceptions of the actual intensities of our relationships, we may (*a*) examine the means of the constants for the individuals, and (*b*) combine all our subsamples to form one large "population" of 2059 pods (6177 locules) for 1906, and 1218 pods for 1907. Table V contrasts the values

obtained from the lumped samples or "population," with the (unweighted) means of the constants for the several individuals.

The means of the three characters are roughly the same for both methods.[8] The standard deviations of both l and o show large differences. The S.D. is dependent upon the differences of the means of individuals as well as upon the variation among the pods of the same plant, hence the mean S.D. of the individuals is less than that for the combined sample.

TABLE V

COMPARISON OF CONSTANTS FOR GENERAL POPULATION WITH THE MEAN VALUES CALCULATED FROM SAMPLES FROM INDIVIDUALS

	Constants for 1906			Constants for 1907		
	Population	Average	Difference	Population	Average	Difference
Mean ovules	8.1588	8.1538	.0050	7.3716	7.4532	.0816
Standard deviation of ovules	1.1244	.7673	.3571	1.2225	.8065	.4160
Mean seeds	.7149	.7165	.0016	.7427	.7418	.0009
Standard deviation of seeds	.8878	.8462	.0416	.9031	.8665	.0366
Mean length of pod	6.3356	6.3374	.0018	6.7570	6.7453	.0117
Standard deviation of length of pod	1.3663	.9773	.3890	1.3385	.9194	.4191
Correlation, length, and ovules	.0652	.1281	.0629	.0261	.1240	.0979
Correlation, length, and seeds	.3522	.3867	.0345	.2019	.3636	.1617
Correlation, length, and $\frac{\text{seed}}{\text{ovule}}$ index	.3418	.....	.....	.2018	.....	.....

Consider the correlations. For both "populations" r_{ls} is positive, and, while not large, is significant in comparison with its probable error. In both series, r_{lo} is positive, but numerically the values are too small to be of any practical significance. Both r_{lo} and r_{ls} are lower for the general sample than for the means of individuals.[9]

[8] Had the number of pods been the same for all plants, or the plants weighted with the number of pods taken, both methods would necessarily have given the same results.

[9] This result is at first rather puzzling. Generally the combination of several series of material raises r, but it is not necessary that this should always be the case. See footnote in a later section.

The regression straight-line formulae are:

For ovules per locule and length: for 1906, $l=5.689+.079\ o$; for 1907, $l=6.546+.029\ o$.

For seeds per locule and length: for 1906, $l=5.948+.542\ s$; for 1907, $l=6.535+.299\ s$.

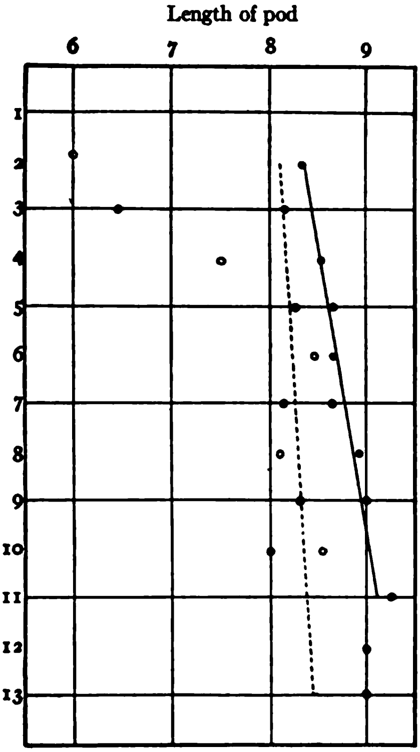


FIG. 2.—Regression of pod length on number of ovules per locule; solid dots and firm line = 1906; circles and broken line = 1907.

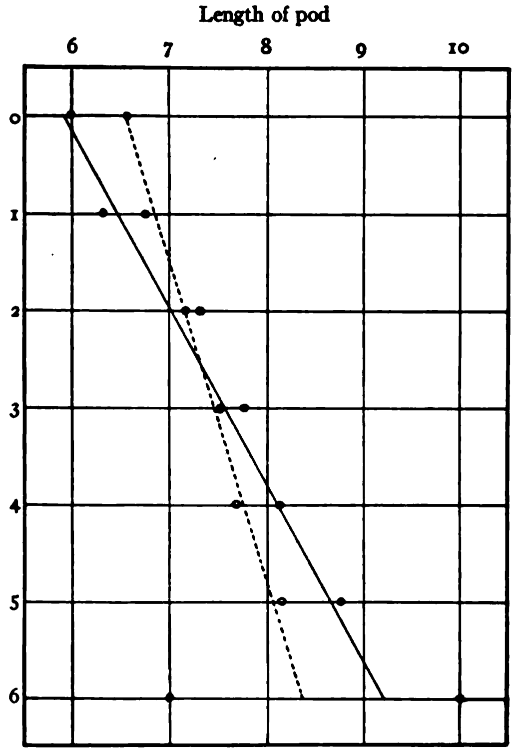


FIG. 3.—Regression of pod length on number of seeds per locule; legend as in fig. 2.

Fig. 2 shows the regression for length on ovules, and fig. 3 that for length on seeds. A straight line seems to represent fairly well the increase in pod length associated with increase in number of seeds. For ovules and length the agreement appears to be very

bad, especially in 1907.[10] These statistical difficulties do not effect the fundamental conclusion to be drawn, and it is in perfect accord with that from the individual shrubs. There is a sensible correlation between length of pod and number of seeds, quite independent of the relationship between number of ovules per locule and length.

TABLE VI

Ovules formed per pod	Length of pod, 1906									
	3	4	5	6	7	8	9	10	11	Totals
15......	..	..	1	..	..	..	..	..	..	1
16......	..	..	..	..	..	..	..	..	..	...
17......	..	1	..	..	2	..	..	..	..	3
18......	..	4	11	9	2	3	..	..	..	29
19......	..	7	16	17	8	8	2	..	..	58
20......	1	8	14	24	19	12	5	..	..	83
21......	..	2	37	35	24	25	7	..	..	130
22......	..	7	30	63	33	27	7	..	..	167
23......	..	14	41	90	69	20	15	2	..	251
24......	..	35	117	167	108	57	27	7	1	519
25......	4	20	45	43	46	23	12	1	..	194
26......	..	12	26	38	34	12	9	3	..	134
27......	..	10	24	30	29	11	3	5	..	112
28......	..	6	24	24	16	15	6	5	..	96
29......	..	7	19	29	27	14	9	4	..	109
30......	1	8	26	29	36	13	5	4	..	122
31......	..	..	4	11	3	4	5	..	..	27
32......	..	..	..	..	4	2	..	1	..	7
33......	..	1	1	1	1	..	..	..	..	4
34......	..	..	1	..	1	..	..	..	..	2
35......	..	..	..	..	..	1	..	..	..	1
36......	..	..	..	..	..	1	..	..	..	1
Totals	6	142	437	610	462	248	112	32	1	2050

C. TOTAL SEEDS PER FRUIT AND FRUIT LENGTH

The normal fruit of *Staphylea* has three locules. In considering the relationship between fertility and length, should we correlate between the number of ovules or seeds maturing per locule, or should we determine the relationship between the total number

[10] One must remember that classes 7, 8, and 9 exert a powerful influence on the slope of the line, while the extreme classes are represented by so few cases that great irregularity is to be expected, even when dealing with as large numbers as we have here. While a straight line does not represent our empirical means at all well, I cannot see that an equation of a higher order would do any better. Perhaps this irregularity accounts in part for the low value of r_{10} calculated from the general samples.

per fruit and the length? The length of the three parallel placentae determines in large measure the length of the fruit. From the purely structural point of view, it would seem logical to compute the relationships for the fertility characters of the individual locules. But in testing the assumption that the developing seed exerts some influence upon the growth of the pod, it is important to determine whether there is a closer interdependence between the length and the total seeds developing per fruit than between the length and the number developing per locule. As a basis for comparison the same relationship for total ovules per fruit must also be computed.

The data are: ovules and length, 1906 (table VI) and 1907 (table VII); seeds and length, 1906 (table VIII) and 1907 (table IX). The constants may at once be compared with those calculated by the other methods in table X. For total ovules and length the agreement with the same relationships for individual locules and length in the population is very close. For total seeds and length, the results are somewhat irregular.[11] The logical comparision would seem to be that of the populations rather than that of population for total seeds and the means of individuals for the numbers per locule. For both series this comparison shows a higher correlation when the total seeds developing are used.

We may now determine whether the slope of a straight line adequately describes the change in pod length associated with different degrees of fertility. Only total seeds and length need be considered. The equations are:

For 1906, $l=5.252+.505\,s$; for 1907, $l=6.186+.256\,s$.

The empirical means and the fitted lines from the above equations are shown graphically in fig. 4. It does not require a trained eye to see that the agreement is not very satisfactory. For the lower seed classes, the length of the fruit increases much more rapidly, and for the higher seed classes much less rapidly than the average rate shown by the slope of the line.

[11] As compared with the population constants for number of seeds per locule and length, both are considerably higher, but when compared with the means of the correlations calculated from the individuals, it appears that the constant for total seeds and length is higher than that for number of seeds per locule and length in 1906, but slightly lower in 1907.

TABLE VII

Ovules formed per pod	Length of pod, 1907								
	4	5	6	7	8	9	10	11	Totals
12	..	..	1	..	..	..	..	..	1
13	..	1	..	..	1	..	..	..	2
14	..	1	3	1	..	..	..	..	5
15	1	1	2	1	..	..	..	..	5
16	..	1	5	5	4	2	..	..	17
17	3	9	13	11	9	5	..	..	50
18	3	15	28	32	24	11	2	..	115
19	..	11	24	39	22	5	2	1	104
20	2	9	23	29	26	7	3	3	102
21	..	12	29	33	18	4	3	..	99
22	2	19	40	19	19	9	3	1	112
23	5	27	33	36	8	11	3	3	126
24	3	55	91	68	31	11	5	1	265
25	2	13	39	17	12	6	2	..	91
26	1	6	14	13	2	2	..	..	38
27	1	2	5	6	7	2	..	..	23
28	..	..	1	7	5	..	..	..	13
29	..	1	2	7	6	2	1	..	19
30	1	..	2	4	6	6	3	..	22
31	..	..	..	1	3	1	..	1	6
32	..	..	..	..	1	..	..	..	1
33	..	..	..	..	..	1	..	..	1
34	..	..	..	..	..	1	..	..	1
Totals	24	183	355	329	204	86	27	10	1218

TABLE VIII

Seeds developing per pod	Length of pod, 1906									
	3	4	5	6	7	8	9	10	11	Totals
0	1	5	2	2	..	..	..	..	..	10
1	5	117	333	344	127	28	2	..	..	956
2	..	17	71	175	150	59	18	2	..	492
3	..	3	19	56	103	65	24	5	..	275
4	..	..	8	19	43	41	31	7	1	150
5	..	..	3	8	26	24	12	1	..	74
6	..	..	1	1	8	16	10	5	..	41
7	..	..	..	2	2	11	8	2	..	25
8	..	..	..	1	1	3	3	5	..	13
9	..	..	..	..	1	..	2	2	..	5
10	..	..	..	2	1	..	..	3	..	6
11	..	..	..	..	..	..	..	..	..	...
12	..	..	..	..	..	1	1	..	..	2
13	..	..	..	..	..	..	..	..	..	...
14	..	..	..	..	..	..	1	..	..	1
Totals	6	142	437	610	462	248	112	32	1	2050

TABLE IX

Seeds developing per pod	Length of pod, 1907								
	4	5	6	7	8	9	10	11	Totals
0	..	2	..	1	..	..	..	..	3
1	21	123	174	138	39	14	10	..	519
2	2	38	99	93	73	17	9	1	332
3	..	15	46	46	41	21	2	4	175
4	..	2	18	24	24	12	..	3	83
5	1	2	9	13	17	7	3	1	53
6	..	..	5	5	4	7	1	..	22
7	..	1	1	3	1	1	2	..	9
8	..	..	2	2	2	5	..	..	11
9	..	..	1	1	1	1	..	..	4
10	..	..	..	..	1	..	..	..	1
11	..	..	..	..	1	..	..	1	2
12	..	..	..	..	..	1	..	..	1
13	..	..	..	..	..	..	..	..	...
14	..	..	..	..	..	..	..	..	...
15	..	..	..	2	..	..	..	..	2
16	..	..	..	1	..	..	..	..	1
Totals	24	183	355	329	204	86	27	10	1218

TABLE X

COMPARISON OF CORRELATIONS FOR LENGTH AND SEEDS AND OVULES PER LOCULE WITH THOSE FOR LENGTH AND TOTAL SEEDS AND OVULES PER FRUIT

Relationship	Constants for two years	
	1906	1907
For ovules and length		
Individual locules, means	.1281	.1240
Individual locules, population	.0652 ± .0148	.0261 ± .0193
Total ovules, population	.0729 ± .0148	.0299 ± .0193
For seeds and length		
Individual locules, means	.3867	.3636
Individual locules, population	.3522 ± .0131	.2019 ± .0185
Total seeds, population	.5888 ± .0097	.3235 ± .0173

To test this matter a little further, I have determined the correlation ratio[12] (η) for comparison with the coefficient of correlation.

For 1906, $\eta = .59724 \pm .00958$; for 1907, $\eta = .37720 \pm .01658$

For 1906, $r = .58881 \pm .00973$; for 1907, $r = .32351 \pm .01731$

$\eta - r = .00843$ $\qquad\qquad$ $\eta - r = .05369$

[12] PEARSON, K., On the general theory of skew correlation and non-linear regression. Draper's Company Research Memoirs, Biometric Series, 2. London. 1905.

As constants describing the degree of interdependence between number of seeds developing and length of pod, there seems little to choose between these. To satisfy ourselves more fully concerning

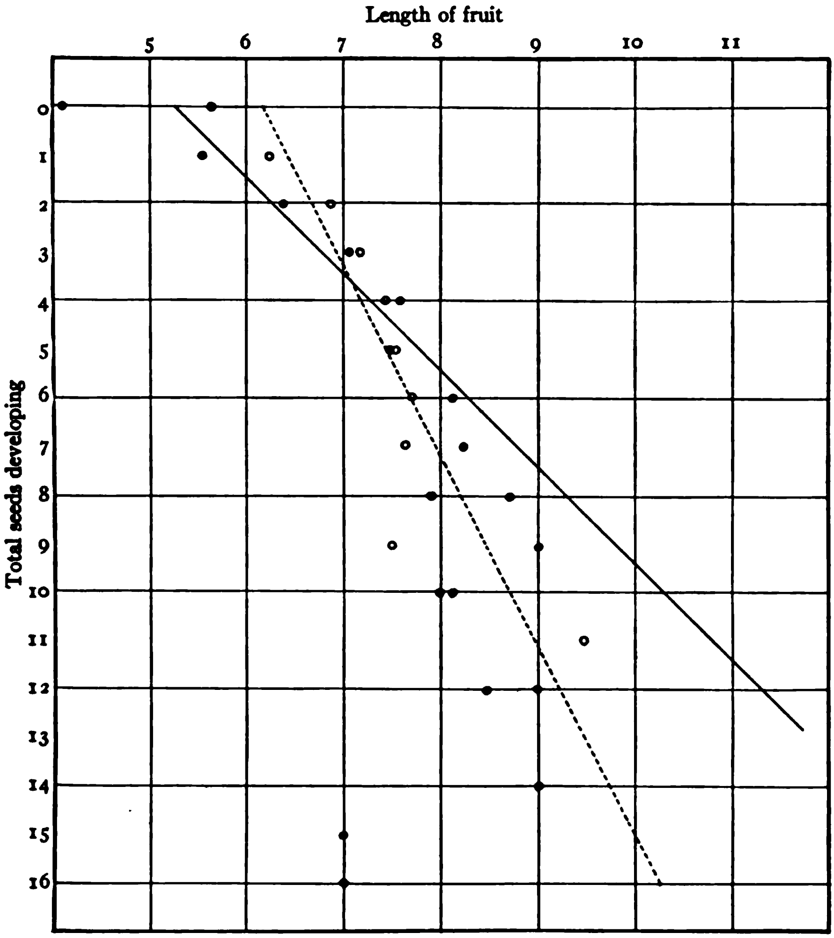


FIG. 4.—Regression of pod length on total number of seeds developing per fruit; solid dots and line = 1906; circles and broken line = 1907.

the rate of change in length of pod, whether it is a simple arithmetical relationship or whether it is some more complex curve, we may calculate ξ and apply BLAKEMAN'S[13] test for linearity of regression.

[13] BLAKEMAN, J., On tests for linearity of regression in frequency distributions. Biometrika 4:332–350. 1905.

$$\xi/E_\xi = \frac{\sqrt{N}}{0.67449} \cdot \tfrac{1}{2}\sqrt{\xi} \cdot \frac{1}{\sqrt{1+(1-\eta^2)^2-(1-r^2)^2}}$$

This gives

For 1906, $\xi = .01000$, $\xi/E_\xi = 3.38$
1907, $\xi = .03762$, $\xi/E_\xi = 5.19$

In both cases $\xi/E_\xi > 2.5$, and regression cannot be safely regarded as linear.[14] Physiologically this indicates that after a certain number of seeds have been formed, the rate of increase in the stimulus to development exerted on the fruit falls off. Something of the same nature has been noticed in *Cercis*,[15] where it appeared that while for the central region of the seed distribution a straight line expressed the change in the pod length very well, pods with a single seed and those with the maximum number of seeds seemed a little smaller in comparison with their number of seeds than the pods of the population as a whole. When better data are available, it will be interesting to investigate this problem in greater detail, but considering the sources of error which have been emphasized above, I see no advantage in further grinding in the mathematical mill. The time would be more profitably spent in collecting other series of data for comparison. The sensibly higher coefficients for total seeds per fruit, as compared with those for seeds per locule, evidence for a direct influence of the seed upon the fruit.

[14] From the graphs one would almost have expected a higher value for ξ/E_ξ, but one of the difficulties in testing linearity of regression in these series is the fact that the frequencies are so concentrated into a few classes. Pods with 1, 2, 3, and 4 seeds form 91.3 per cent of the total in 1906, and 91.1 per cent in 1907. With so few pods falling in the extreme classes, it is difficult to get arrays sufficiently large to give trustworthy averages for testing the goodness or fit of means to any equation. In 1906 there are only 15 classes for 2050 pods, while in 1907 there are 17 classes for 1218 pods. Consequently the mean number of pods per array is less in 1907, and the probable error attaching to these means is greater, thus increasing the value of η by an amount depending on the magnitude of the probable errors. For 1906 the average number for arrays with entries is 157.7 pods, while for 1907 it is only 81.2. The probable errors of the means of arrays, therefore, is much higher in 1907 than in 1906, but there is no method of freeing η from their influence; perhaps these facts explain why ξ/E_ξ is greater in 1907 than for 1906.

[15] Compare the figure in BOT. GAZ. **50**:122. 1910.

CARNEGIE STATION FOR EXPERIMENTAL EVOLUTION
COLD SPRING HARBOR, N.Y.

CONTRIBUTIONS FROM THE ROCKY MOUNTAIN HERBARIUM. X

NEW PLANTS FROM IDAHO[1]

AVEN NELSON

Carex owyheensis, n. sp.—Plants wholly glabrous, single or in small tufts from cormlike rootstocks with an abundance of fibrous roots: culm rather slender, inconspicuously striate, 3–5 dm. high: leaves bright green, few to several, mostly basal with one near the middle of the culm and one or two foliar bracts above, rather short and broad (5–15 cm. long and 6–12 mm. broad), flat, often with acute involute apex: spikes 3–5, in a capitate terminal cluster, and with one or two more or less remote spikes in the axils of foliar bracts, 12–22 mm. long; the bracts of the terminal cluster from lance-acuminate to broadly ovate and obtuse; terminal spike staminate above only: stigmas 3; perigynium membranous, not strongly nerved, narrowly ovate, tapering gradually into the beak which is shorter than the body, pale green with small reddish brown dots below and with the two short, rather soft teeth of the beak dark reddish brown, about 5 mm. long; scale ovate-oblong, obtuse, thin, the pale green center one-nerved, the margins dark reddish brown, much shorter than the perigynium: achene trigonous-ovoid.

This is probably nearest to *C. Raynoldsii* Dew. as regards the technical characters, but in the color and in the grouping of the terminal spikes it is suggestive of *C. viridis* Dew. and *C. multinoda* Bailey. It was secured by MACBRIDE at Silver City, in the Owyhee Mountains, in marshy ground, July 20, 1910, no. 442.

Calochortus cyaneus, n. sp.—Glabrous and somewhat glaucous, rather slender, 3–4 dm. high: bulb small, ovate to oblong, more or less covered with dead flaky scales as is also the base of the nearly straight stem: leaves 3–5, including the 1 or 2 floral ones, narrowly linear, involute, somewhat expanded at the sheathing base, 6–10 cm.

[1] The first paper dealing with the collections of Mr. J. FRANCIS MACBRIDE in Idaho appeared in BOT. GAZ. 52:261–274. 1911, where there is also a brief outline of the field work and the field covered.

long or the basal one longer: flowers disproportionately large: sepals narrowly linear-lanceolate, 5–6 cm. long, tapering very gradually into the slender tip, bluish green with green midrib and white scarious margins: petals obovate-cuneate (either narrowly or broadly), rather abruptly rounded into the short lanceolate acute tip, as long as or somewhat longer than the sepals, delicate in texture, pale blue with greenish tinge and a narrow green stripe from apex to the gland; gland small, within 5 mm. of the base, bordered at sides and apex with flat yellow hairs, the upper four-fifths of the petal wholly glabrous: anthers yellow, 12–14 mm. long, exceeding the filaments: capsule narrow, nearly as long as the sepals.

Probably most nearly related to *C. macrocarpus* Dougl., from which it is easily distinguished by its slender habit, color of flowers and anthers, and the nearly glabrate petal face. Secured by MACBRIDE on the dry slopes of the foothills of the Boise Mountains, June 18, 1910, no. 268.

Arabis arcoidea, n. sp.—Perennial from a low multicipital caudex surmounting the rather slender woody taproot: stems few to several, simple, slender, erect, 2–5 dm. high, including the long raceme, rather densely short-hirsute below, glabrate above, the pubescence simple or branched (not stellate): leaves entire, crowded-rosulate on the crowns, narrowly linear-spatulate, tapering gradually into the very slender base, 4–6 cm. long (including the base), grayish green with a dense substellate pubescence; stem leaves several, auriculate-clasping at base, smaller, linear, rather distant, gradually reduced to small glabrate bracts above: inflorescence, wholly glabrous: sepals oblong, obtuse, with greenish base and thin purplish tips: petals purplish to violet, spatulate, about 8 mm. long, twice as long as the sepals: stamens scarcely longer than the sepals: pods glabrous, narrowly linear (less than 1.5 mm. broad), 4–6 cm. long, arcuate spreading, on ascending pedicels 5–10 mm. long; seeds in one row, very thin, with wings more than half as broad as the body.

I am unable to refer this to any close ally. If one had only the young plants, one would refer it by reason of the aspect of the basal leaves to *A. canescens* Nutt., to which it may be somewhat related in spite of the very different pods and pubescence. Secured by MACBRIDE at New Plymouth, Canyon County, on dry sandy soils, May 21, 1910, no. 87.

Lupinus multitinctus, n. sp.—Strongly tufted, 4–7 dm. high: stems sparingly branched above, leafy above, the lower stem leaves and most of the root leaves wanting at maturity, from glabrate to minutely pubescent: leaves green, but silvery-silky below, and sparsely pubescent above; petioles slender, the radical and lower cauline several times longer than the leaflets, the uppermost about equalling the leaflets; leaflets 7–11, broadly linear, tapering to the acute ends, 3–5 cm. long: racemes rather slender, dense, 6–12 cm. long; flowers many colored, ranging from nearly white through various shades of yellow to pinks and purples, the individual flowers usually bi- or tri-colored, in 3–5-flowered verticils, on short pedicels which in fruit become 5–8 mm. long; bracts linear, nearly as long as the calyx, caducous: calyx appressed-silky, with thick spur as long as its tube, its lips merely short entire teeth: standard obscurely if at all pubescent, the blade orbicular, about 10 mm. broad, the short base spurred and extending to the base of the calyx spur; wings obovate-elliptic, very delicate, beautifully cross-veined on one side; keel narrow, its darker tip rather conspicuously extruded: pods broad and very flat, densely silvery-silky, with subappressed pubescence, 2–5-seeded.

This new member of the CALCARATI section will most readily be distinguished from the relatively few other spurred species by the beautiful and singular variation in colors shown by the flowers of even a single clump. Like the other members of the section, this shows a slight ciliolation on the middle of the keel. From *L. laxiflorus* Dougl. it may be distinguished by its entire calyx lobes and the more numerous and narrower leaves. No. 114, from steep, north slopes, near Big Willow, near Falk's Store, Canyon County, by MACBRIDE, is typical.

Lotus Macbridei, n. sp.—Glabrous perennial from a short narrowly conical taproot with enlarged crown and numerous semi-fleshy fibrous roots: stems slender and crowded on the crown, widely spreading, or prostrate with assurgent tips, 15–50 cm. long: leaves mostly trifoliate, the petioles 3–8 mm. long; leaflets narrowly oblong or oblanceolate, acute or obtuse, 6–16 mm. long; stipules resembling the leaves and about as large, oblong-lanceolate: flowers a pure yellow, in close almost capitate terminal clusters of 3–7: calyx campanulate, subsessile on the short obconical base,

its lobes narrowly linear-subulate, 2–3 mm. long, as long as the tube: petals obscurely dark veined, with pale claws; the standard about 1 cm. long, its blade suborbicular; the wings as long, obovate with short slender claw; the keel rather narrow, with broadly subulate tip: pods linear, straight, the sutures rather prominent, 20–25 mm. long and 2 mm. broad.

The first collection of this species was secured by MACBRIDE in 1909 and was indicated as new at that time. However, it was deemed wise to withhold publication until a full series of specimens could be secured. No. 227, collected June 7, 1910, is taken as the type. Its range seemed to be rather restricted, but it was found to be quite abundant on wet grassy bottom lands near Falk's Store, in Canyon County.

Astragalus adanus, n. sp.—Root rather large, woody, with branched subterranean crown: stems numerous, rather slender, glabrate, rather coarsely and few-striate, simple, 2–4 dm. high: leaves numerous, narrow, with 13–25 leaflets; the basal 15–20 cm. long including the long almost filiform petiole; cauline leaves shorter and with shorter and slightly stouter petiole; leaflets thin, from oblong to broadly obovate, 7–14 mm. long, glabrous above, sparsely appressed pubescent beneath; stipules short, scarious, ovate-lanceolate: racemes 1–3, few-several-flowered (5–15), axillary in the uppermost leaves on stout peduncles 10–18 cm. long, in fruit much surpassing the subtending leaves; flowers probably ochroleucous: calyx seemingly scarious in part, with scattering black hairs near the base: pod 1-celled, neither suture intruded, thick cartilaginous, the sutures rather prominent, somewhat flattened dorsally, narrowly ovoid with short-acuminate incurved compressed apex, at maturity distinctly cross-ribbed, about 1 cm. long.

This makes the fourth species in the section PECTINATI, the others being *A. pectinatus* (Hook.) Dougl., *A. Grayi* Parry, and *A. nudus* Wats. The leaflets in this species, as in the others, are indistinctly jointed to the rachis, but they are not linear. Since *A. nudus* has violet blue flowers, there seems to be no characters left upon which to rest RYDBERG'S genus *Ctenophyllum* (one of his 17 Colorado segregates of *Astragalus*) except the mode of leaf attachment. The cross-wrinkling of the pods crops out in others of the segregates as well.

The new member of this group comes from the Boise Hills, no. 260 by MACBRIDE, June 18, 1910. The name is based upon the name of the county, which is said to be of Indian origin.

Astragalus boiseanus, n. sp.—Tufted: stems several to many from a woody root, simple, erect, 2–4 dm. high, striate, sparingly appressed-pubescent or glabrate: leaves ascending or suberect, 5–10 cm. long (including the short petiole); leaflets 13–25, oblong, obtuse or slightly emarginate, with an obscure mucro, glabrate above, sparsely appressed strigose beneath, 10–15 mm. long: racemes short, crowded, few-flowered (5–10), on stout axillary peduncles which in fruit elongate to form a flat-topped corymb: calyx tubular, nigrescent, its short lobes subulate: pod stipitate, nearly straight, about 2 cm. long, abruptly acute or acuminate, suberect on the divaricate or ascending pedicel and stipe, the dorsum depressed and with a broad sulcus so intruding the suture as to form a two-celled pod, ventral suture prominent; stipe stoutish, 1 cm. or more long, twice to thrice as long as the calyx.

This has long been referred to *A. arrectus* Gray, to which indeed it is closely related, and the descriptions are alike in many particulars. The plant proposed as new, however, may readily be distinguished by its stouter habit, its shorter leaves and fewer leaflets, its crowded flat-topped appearance in fruit, and more unerringly by the long stipes. In *A. arrectus* the stipe and calyx are subequal, and the more numerous pods in the slender fruiting raceme are more or less appressed to the rachis. Wholly typical of GRAY's species and nicely representing it are C. V. PIPER's specimens as follows: Pullman, Wash., July 3, 1903; Palouse Hills, June 30, 1897.

The segregate seems to be the commoner form, and apparently its range is from southern Idaho to Utah and Arizona, but as one may readily be mistaken about specimens in blossom only, I cite only fruiting specimens: C. N. WOODS, no. 4, Caldwell, Idaho, May 1910; FRANCIS MACBRIDE, no. 257, Boise hills, June 18; no. 112 (type), Big Willow, May 27, 1910. The much earlier date at which *A. boiseanus* matures indicates its distinctness from *A. arrectus*.

Astragalus Booneanus, n. sp.—Acaulescent, the woody root with several to many crowns: leaves 6–9 cm. long, crowded on the crowns, hoary with a soft dense tangled (rather than appressed) pubescence, on petioles from one-half to nearly as long as the blade; leaflets 13–21, linear-lanceolate or narrowly oblong, 1 cm. or less long, the lower often alternate: scapes shorter than the leaves, capitately few-flowered: calyx tubular; the tube about 1 cm. long, soon distended by the pod and at length deciduous; its teeth linear, 3 mm. long: corolla violet or purple, the standard 20–25 mm. long,

the blade ovate, the claw broad, channeled or folded, tapering gradually to the base, much longer than the blade; wings oblong, much shorter than the slender claw; the very narrow claws of the keel petals twice as long as their blades: pod thick-coriaceous, obcompressed, ovate, curved, the impressed dorsal suture nearly or quite meeting the ventral, white-hoary with a long soft dense tangled pubescence which is persistent.

This has passed for *A. glareosus* Dougl. and is another case in which species are difficult to distinguish by descriptions alone. These two may be at once separated, however, by the character of the pubescence. In *A. glareosus* it is silky with incumbent appressed hairs, while in *A. Booneanus* it is much denser, looser, and tangled. The pods also are distinguishing in that in the former they are glabrate at maturity; in the latter the shaggy pubescence is permanent.

The species rests upon several very representative collections as follows: President W. J. BOONE, of the College of Idaho, at Caldwell, no. 2, in whose honor the species is named; C. N. WOODS, supervisor Sawtooth National Forest, Hailey, nos. 5 and 25*a;* MERRILL and WILCOX, Leckie, Wyo., no. 583; and J. FRANCIS MACBRIDE, Falk's Store, Idaho, no. 57.

LIGUSTICUM TENUIFOLIUM **dissimilis,** n. var.—What is at least an interesting variety of this species was secured by MACBRIDE in his no. 677, from the Trinity Lake region, August 29, 1910. At first glance one would not suspect any close relationship, but the technical characters show that size and aspect may be misleading. The following points may be enough to distinguish this variety:

Stem naked except for one or at most two reduced bractlike leaves near the inflorescence, 3–5 dm. high: leaves bright green, ternate then pinnate, 1–2 dm. long; petiole one-third to one-half the length; leaflets narrowly to broadly ovate, 15–25 mm. long, pinnately cleft into linear-lanceolate lobes 8–14 mm. long: rays 9–14, 25–40 mm. long; pedicels 8–12 mm. long: fruits essentially as in the species but larger, with longer and stouter stylopodium.

Cornus instoloneus, n. sp.—*Cornus stolonifera* of authors as to western and intermountain specimens; *Suida stolonifera riparia* Rydb. Bull. Torr. Bot. Club 31:573. 1904; *Suida riparia* in herb; not *Cornus riparia* Rafin.

MACBRIDE having collected a fine series of specimens of this well known species, it became necessary, before labeling for distribution, to look into its present nomenclatural standing. In doing so the writer became convinced that RYDBERG is right in separating the eastern and the western forms. Not only is the western one not stoloniferous, but the leaf distinction is even stronger than as stated by RYDBERG. In the eastern plant the veins are large and cord-like, and appear singularly superficial, a character that does not appear at all in any one of the numerous western specimens examined.

Sambucus ferax, n. sp.—*S. glauca* Nutt. in part. So much has been written on *S. glauca*, and the descriptions by SARGENT (*Man. trees N. Am.* p. 807. 1905) and by BRITTON (*N. Am. trees*, p. 852. 1908) are so full that the plant here proposed as a segregate may best be discriminated by contrast:

It is always a shrub (never treelike) 1–2 dm. high, rarely more: it blossoms and fruits on the season's shoots which have sprung up from the ground as well as on the shoots from the shrubby stems (*S. glauca* is a tree with definite trunk and rounded top): the twigs are glabrous from the first, not pubescent; the pith is slightly brownish, not white: the leaves are smooth from the first and green, not yellowish green: the lanceolate-acuminate leaflets are 7–11, not 5–9, and the teeth are not callous-tipped; they also average much longer, being frequently 15 cm. or more long: the inflorescence is mostly very large, often 3 dm. broad instead of half that size; instead of a single terminal 5-rayed peduncle there are usually or often three 5-rayed peduncles: the flowers are distinctly larger, often 6–7 mm. instead of 3 mm. broad: the fruit is borne in the greatest abundance and seems to observe no regular season, flowers being still seen in great profusion when the first fruits are wholly mature.

The above differences seem sufficient to warrant separating one of the interior shrubby forms from the tree form of the Pacific states. That all the shrubs of the interior should be so separated, I am not prepared to say, but it will not be surprising if careful field study shows that the shrub so common in the interior mountain states is also distinct as well as the one here considered.[2]

The type is MACBRIDE's no. 631 from Trinity, on moist slopes, August 23, 1910, when flowers and fruit were both abundant. The large handsome glaucous berries are excellent for pies or jelly.

[2] Since writing these notes, I have received a copy of M. E. JONES' paper in which the shrub here referred to is published as *S. decipiens* Jones, Bull. Univ. Montana, Biol. Series 15: 46. 1910.

Eupatorium occidentale **decemplex**, n. var.—Tufted, the slender stems from the branches of the rhizomatous woody caudex, 3–5 dm. high, pale, slightly puberulent: leaves alternate, rather numerous above, smaller, more distant downward or wanting at base, bright green, thin, obscurely scabro-puberulent, ovate, obtuse or acute, rounded or broadly cuneate at base, short-petioled, rather strongly reticulate veined below, entire to rather coarsely dentate: heads several–many, in a short foliose narrow cymose panicle, puberulent on the bracts and pedicels: involucre tubular-campanulate, 3–4 mm. high, barely half as high as the disk; its bracts linear-oblong, subacute, about 10 and the flowers about the same number, scarcely striate (a midrib and sometimes a pair of faint nerves): corolla rose color, narrowly tubular, about as long as the few scabrous (about 20) pappus bristles and longer than the linear 5-nerved brown achenes.

I have characterized in detail because descriptions of the species available in the manuals are either too brief or else have been gradually so modified as to include some of the forms that seem worthy of being listed separately. The variety here proposed differs primarily in its slender stems, thin bright-green leaves, and the marked uniformity in the number of involucral bracts and rose colored flowers (ten of each). The original collections of the species had 15–25 bracts with white or ochroleucous flowers of about the same number as the bracts.

The more southern form of this, which has so long passed as a variety of *E. occidentale*, is well worthy of specific rank, and I wish so to list it here.

Eupatorium arizonicum (Gray), n. sp.—*E. occidentale arizonicum* Gray, Syn. Fl. 1:101. 1886. This is at once distinct by its aspect, the stoutish stems, more or less branched from the base up, the thickish pale leaves with rather indistinct venation, and more particularly by the several corymbose-cymose clustered whitish flowers on the more or less elongated branchlets, giving a corymbose effect to the whole inflorescence. The leaves are opposite and fairly uniformly truncate-subcordate to deeply cordate at base.

E. arizonicum is far more closely allied to *E. ageratoides* than to *E. occidentale*. This species seems to range from New Mexico to Arizona and north into Nevada and Utah.

Macronema aberrans, n. sp.—Roots woody, rather slender, creeping in rock crevices, their crowns more or less branched: stems

herbaceous, slender, erect, only 5–10 cm. high, glandular-pubescent: leaves granular-glandular-viscid, obovate or oblong or broadly oblanceolate, the blades 1–3 cm. long, obtuse or subacute, mostly sparsely cuspidate-toothed on margin; the lower tapering cuneately into a slender petiole as long as the blade: heads 1–4, 9–14 mm. high, subsessile and subtended by the upper leaves and bracts; involucral bracts broadly linear, in 3 or 4 rows, acute and subcuspidate, green and glandular-viscid at apex, pale and carinate at base: rays wanting; disk flowers numerous, slender: achene cylindric-fusiform, pubescent, about 3 mm. long, about one-third as long as the corolla, which barely exceeds the scabrous pappus.

With the admission of *M. grindelioides* Rydb. and now this species to the genus *Macronema*, the characters of the genus must be modified so as to include toothed as well as entire leaves, and the involucral bracts in even 3–4 series.

No. 641, by MACBRIDE, from Trinity Lake region, Elmore County, August 27, 1910, is the type.

Machaeranthera magna, n. sp.—Grayish-tawny with a minute puberulence and granular-viscid, more strongly upward: stems stout, few to several from a stout biennial root, branched upward and leafy, naked below, 5–10 dm. high: leaves linear, very numerous, more or less involute, 1–3 cm. long, abruptly apiculate with a minute white cusp, margins entire or occasionally a few scattering larger leaves occur and these are sparsely few-toothed: heads numerous on the branched upper half of the plant, terminal and racemosely or spicately disposed on the branchlets, subtended by several foliar bracts: involucre broadly turbinate, 8–10 mm. high, almost as broad, shorter than the disk; its bracts in several series, erect at first but the dark tips at length squarrose or reflexed, minutely white-puberulent and viscid: rays 15–20: achenes densely short-pubescent, shorter than the fuscous pappus which equals the corolla.

At first glance one might think this a gigantic *M. viscosa* Greene if it were not for the small multitudinous linear evidently pubescent leaves, and the unusual viscosity which extends to most of the plant instead of a part of the

d,

.'s

ERIOPHYLLUM GRACILE (Hook.) Gray.—This was listed by PIPER in his *Flora of Washington* as a synonym of *E. integrifolium* (Hook.) Greene (*E. multiflorum* [Nutt.] Rydb.). This he apparently did simply because no one until now has again collected it since TOLMIE's original specimens, from somewhere in the Snake River country, were secured. MACBRIDE's no. 137 seems to perfectly represent *E. gracile* as originally described, and I therefore suggest that this name must be retained.

Carduus magnificus, n. sp.—Biennial, very tall (1–2 m.) and strict, moderately stout, or rather slender: stem purplish, often strikingly so, strongly striate, moderately pubescent with long flat jointed straggling hairs, very leafy: leaves glabrate above, tomentose beneath, broadly linear in outline, 1–3 dm. long, the bordered midrib 7–15 mm. wide, the rather numerous spinous pinnae 12–25 mm. long, 1–3-lobed or parted, the lobes mostly lanceolate or broader: heads few to several, racemosely disposed on short branchlets successively shorter to sessile above, 4–6 cm. high and broad, subtended by several to many linear purplish foliar bracts which often well surpass the heads: involucral bracts numerous, in several series, green but sparsely pubescent on the margins; the outer with rather weak spines; the inner with elongated, dilated, crimped or fringed tips: flowers a rich purple, very numerous and slender; corolla tube scarcely as long as the limb which is cleft halfway into 5 filiform lobes: styles well exserted: achenes 5–6 mm. long, narrowly oblong or linear-spatulate, brown, glabrous or almost polished, the conspicuous stylophore encircled by a raised yellowish white collar-like border: pappus bristles very soft, sparsely and delicately plumose except the tips.

This falls into the section ECHINAIS Cass, DC., and the section CARLINOIDES of RYDBERG's Colorado list, but it evidently is not closely related to any of the species heretofore known. MACBRIDE reports this plant as scattering on a wet saline flat near Falk's Store, Canyon County, Idaho. No 271, June 22, 1910, is the type.

UNIVERSITY OF WYOMING
LARAMIE, WYOMING

THE RELATIVE WILTING COEFFICIENTS FOR DIFFERENT PLANTS[1]

LYMAN J. BRIGGS AND H. L. SHANTZ[2]

The wide range in moisture content of different soils at the time of wilting of the plant cover appears to have been first clearly recognized by SACHS[3] in 1859. Later investigators, in extending this work, concluded that not only do soils show a wide range in moisture retentiveness, but that different groups of plants differ widely in their ability to reduce the moisture content of a given soil. Thus, the experimental work of GAIN,[4] HEINRICH,[5] HEDGCOCK,[6] and CLEMENTS[7], all indicates considerable variation in the moisture content of the soil at the time of wilting of different plants, which has been interpreted to mean that some plants are capable of reducing the moisture content of a given soil to a lower point than others; in other words, that the "non-available moisture" varies according to the kind of plant used as an indicator. In fact, this is the view which is usually presented in many of the standard works on plant physiology and plant ecology.

The difference exhibited by plants in this respect has also been

[1] Published with the permission of the Secretary of Agriculture.

[2] For discussion of methods and additional matter, see BRIGGS, L. J., and SHANTZ, H. L., A wax seal method for determining the lower limit of available soil moisture. BOT. GAZ. 51:210–219. 1911.

The wilting coefficient for different plants and its indirect determination. U.S. Department Agric. Bur. Pl. Ind. Bull. 230. 1912.

The wilting coefficient and its indirect determination. BOT. GAZ. 53:20–37. 1912.

[3] SACHS, J., Berichte über die physiologische Thätigkeit an der Versuchstation in Tharandt. Landw. Versuchs. Stat. 1:235. 1859.

[4] GAIN, E., Action de l'eau du sol sur la vegetation. Rev. Gen. Bot. 7:73. 1895.

[5] HEINRICH, R., Zweite Bericht über die Verhaltnisse und Wirksamkeit des Landwirtshaftlichen Versuchs-Station zu Rostock. 1894: 29.

[6] HEDGCOCK, G. G., The relation of the water content of the soil to certain plants, principally mesophytes. Bot. Surv. Neb. VI. Studies in the vegetation of the state. II. 1902: 5–79.

[7] CLEMENTS, F. E., Research methods in Ecology. 1905: 30.

considered to be an important factor in drought resistance, the additional supply of water thus made available to some plants being supposed to be sufficient to carry them through a dry period when other plants would succumb to drought. With this point of view in mind, the present writers have made an extensive series of determinations with a number of plants, including native plants from semi-arid and arid regions, to determine the variation exhibited in their ability to reduce the moisture content of the soil before permanent wilting takes place. The results of these investigations have led us to conclude that the variation exhibited by different plants is much less than has heretofore been supposed, and that it is insignificant compared with the range in moisture retentiveness exhibited by different soils.

The observations given in the following table embrace about 1300 observations made with plants growing in 20 different types of soil. The actual wilting coefficients as observed range from less than 1 per cent in the case of the dune sands to 17 per cent for the clay loam. In order to reduce the results of these observations to a comparable basis, the relative wilting coefficient has been determined by taking the ratio of each individual determination to the mean of all the determinations made with that soil. If the wilting coefficient for a particular plant is higher than the average, the ratio will be greater than unity. If, on the other hand, a plant is capable of reducing the moisture content below the point attained by other varieties before wilting occurs, then the ratio will be less than unity. In this way it is possible to combine all the observations made upon different soils and to determine the extent to which any particular plant is able to reduce the soil moisture content below the point reached by other plants before wilting occurs.

It will be seen from table I that the extreme values of the relative wilting coefficient for all plants upon which six or more determinations are made are represented by 0.92 for Japan rice and 1.13 for *Colocasia*. The latter plant has an extremely coarse root system, the fine fibrous roots so characteristic of the grasses being wholly absent. A plant with a root system of this kind does not reduce the water content of the soil uniformly. At the time

TABLE I

THE RELATIVE WILTING COEFFICIENTS FOR DIFFERENT VARIETIES

Plant	Variety	No.	No. of obs.	Mean ratio	Probable error of mean ratio	Probable error of single observation
Zea mays...	Boone Co. white	United States	..	..	.....	.....
	....	selection 119...	33	1.00	0.007	0.038
	Esperanza.....	M 66.........	16	1.06	0.013	0.052
	Minn. 13......	United States selection 133...	3	1.03	.....	.....
	Hopi.........	A 7..........	3	1.05	.....	.....
	United States selection....	165...........	4	1.00	.....	.....
	Indian flint....	....	3	1.08	.....	.....
	Northwestern dent........	....	4	1.09	.....	.....
	Laguna.......	....	4	1.05	.....	.....
	Chico.........	M 72.........	2	1.06	.....	.....
	Iowa silver mine........	....	3	1.06	.....	.....
	Chinese.......	S.P.I. 22308 ..	3	1.03	.....	.....
Andropogon sorghum...	White durra...	S.P.I. 24997...	17	0.94	0.012	0.052
	Dwarf milo....	S.P.I. 24970...	17	0.994	0.017	0.072
	Red amber ...	S.P.I. 17543...	7	0.94	0.007	0.044
	Black amber...	Minn. 341.....	12	1.00	0.026	0.089
	Red kafir......	S.P.I 24985....	3	1.01		
	Black-hull kafir........	S.P.I. 24975...	3	1.03	.....	.....
	Dagdi durra...	S.P.I. 9856....	3	1.02	.....	.....
	Black-hull kowliang.....	G.I. 310.......	3	1.03	.....	.....
	Brown kowliang.....	S.P.I. 24993...	1	1.04	.....	.....
Chaetochloa italica.....	Kursk.........	S.P.I. 22420...	27	0.954	0.008	0.040
	Common......	S.P.I. 22423...	6	0.96	0.011	0.027
	Siberian.......	S.P.I. 21076...	6	1.01	0.009	0.023
	German.......	S.P.I. 26845...	3	1.00	.....	.....
	Chaetochloa italica.......	S.P.I. 21073...	3	1.04	.....	.....
Panicum miliaceum.	Proso.........	G.I. 72.......	3	0.99	.....	.....
Triticum durum....	Kubanka......	G.I. 1440.....	593	1.00	0.0021	0.051
	Kubanka......	G.I. 1354.....	3	0.94	.....	.....
	Kubanka......	G.I. 2246.....	3	0.97	.....	.....
	Yellow gharnovka.......	S.P.I. 26008...	3	0.94	.....	.....
	Yellow gharnovka.......	G.I. 1444......	3	0.96	.....	.....
	Pelissier	G.I. 1584.....	3	0.97	.....	.....
Triticum vulgare....	Bluestem......	Minn. 169.....	28	0.96	0.0066	0.035
	Turkey red....	G.I. 1558.....	11	0.99	0.0116	0.038
	Fretes........	S.P.I. 19239...	3	0.94	.....	.....
	Power's fife....	G.I. 3025......	3	0.95	.....	.....

TABLE I—*Continued*

Plant	Variety	No.	No. of obs.	Mean ratio	Probable error of mean ratio	Probable error of single observation
Triticum dicoccum	Spring emmer	S.P.I. 19907	3	1.07	......	......
Avena sativa	Kherson	G.I. 459	15	1.03	0.0149	0.058
	Swedish select	S.P.I. 24877	13	0.984	0.009	0.033
	Canadian	S.P.I. 12880	3	0.96	......	......
	75 day	G.I. 337	3	1.02	......	......
	60 day	G.I. 639	3	1.04	......	......
	Big 4	G.I. 558	3	1.03	......	......
	Burt	S.P.I. 24670	3	0.93	......	......
	Red rust proof	G.I. 458	3	0.92	......	......
Hordeum distichon	White smyrna	G.I. 195	3	0.94	......	......
	Hannchen	G.I. 531	18	0.98	0.011	0.047
	Unknown	....	16	0.98	0.013	0.034
Hordeum vulgare	Beldi	G.I. 190	14	0.97	0.013	0.054
	Telli	G.I. 194	3	0.92	......	......
	Mariut	G.I. 261	3	0.95	......	......
	Oderbrucker	S.P.I. 26105	2	0.92	......	......
	Hull-less	S.P.I. 12709	1	0.91	......	......
Secale cereale	Giant winter rye	....	19	0.94	0.011	0.049
Oryza sativa	Japan	G.I. 1642	15	0.92	0.014	0.054
	Carolina golden	G.I. 1645	3	0.96	......	......
	Honduras	G.I. 1643	3	1.03	......	......
Gramineae	Bromus inermis	....	33	0.94	0.005	0.028
	Agropyron Smithii	....	11	1.03	0.013	0.043
	Agropyron tenerum	....	15	0.99	0.013	0.052
	Agropyron cristatum	....	6	0.96	0.013	0.032
	Elymus canadensis	....	3	1.00	......	......
	Stipa Vaseyi	....	3	0.99	......	......
	Sitanion hystrix	....	3	0.97	......	......
	Aristida longiseta	....	2	1.00	......	......
	Bouteloua oligostachya	....	1	1.01	......	......
Leguminosae	Medicago sativa	S.P.I. 25695	33	0.98	0.006	0.035
	Vicia villosa	S.P.I. 25935	17	1.04	0.013	0.053
	Vicia faba	S.P.I. 15428	23	1.02	0.016	0.078
	Pisum arvense	S.P.I. 19389	28	1.05	0.012	0.064
	Melilotus alba	S.P.I. 21216	8	1.03	0.012	0.033
	Vicia fulgens	S.P.I. 21502	6	0.93	......	......
	Vicia atropurpurea	S.P.I. 18132	3	1.05	......	......
	Vicia ervilia	S.P.I. 16137	3	0.92	......	......
	Cicer arietinum	S.P.I. 24322	3	0.93	......	......
	Vigna unguiculata	S.P.I. 26497	3	0.98	......	......
	Trifolium pratense	....	5	1.04	......	......

TABLE I—*Continued*

Plant	Variety	No.	No. of obs.	Mean ratio	Probable error of mean ratio	Probable error of single observation
Leguminosae	Onobrychis viciaefolia. . .	S.P.I. 24931. . .	3	1.00	. . . . . .	. . . . . .
	Lupinus pusillus	. . . .	2	0.97	. . . . . .	. . . . . .
Cucurbitaceae.	Cucurbita pepo	. . . .	15	1.01	0.018	0.073
	Cucumis sativa.	. . . .	1	0.90	. . . . . .	. . . . . .
	Cucumis melo. .	. . . .	1	1.04	. . . . . .	. . . . . .
Lycopersicon esculentum	Livingston.	. . . .	17	1.05	0.011	0.043
	Stone.	. . . .	3	1.08	. . . . . .	. . . . . .
Colocasia. . . .	. . . .	S.P.I. 21190. . .	19	1.13	0.015	0.059
Mesophytes. .	Ipomoea purpurea.	. . . .	3	1.11	. . . . . .	. . . . . .
	Plantago lanceolata.	. . . .	2	1.06	. . . . . .	. . . . . .
	Citrus limonum	. . . .	1	0.96	. . . . . .	. . . . . .
	Abutilon striatum.	. . . .	2	0.91	. . . . . .	. . . . . .
	Gossypium hirsutum.	. . . .	2	1.05	. . . . . .	. . . . . .
	Coleus.	. . . .	5	0.99	. . . . . .	. . . . . .
	Lactuca sativa. .	. . . .	3	1.11		
	Solanum tuberosum.	. . . .	3	1.06	. . . . . .	. . . . . .
	Fagopyrum vulgare.	. . . .	1	1.05	. . . . . .	. . . . . .
	Beta vulgaris. .	. . . .	3	1.06	. . . . . .	. . . . . .
	Linum usitatissimum.	. . . .	2	0.99	. . . . . .	. . . . . .
	Brassica napus	. . . .	3	0.94	. . . . . .	. . . . . .
	Amaranthus retroflexus. . .	. . . .	5	1.01	. . . . . .	. . . . . .
Xerophytes. .	Grindelia squarrosa.	. . . .	4	1.08	. . . . . .	. . . . . .
	Vernonia marginata.	. . . .	3	1.04	. . . . . .	. . . . . .
	Artemisia gnaphalodes. . . .	. . . .	6	1.06	. . . . . .	. . . . . .
	Pachyphytum aduncum. . . .	. . . .	1	1.03	. . . . . .	. . . . . .
	Echeveria pubescens	. . . .	1	1.10	. . . . . .	. . . . . .
	Nopalea coccinelifera.	. . . .	1	1.03	. . . . . .	. . . . . .
Hydrophytes.	Ranunculus septentrionalis. .	. . . .	2	0.98	. . . . . .	. . . . . .
	Juncus balticus	. . . .	1	1.07	. . . . . .	. . . . . .
	Nasturtium. . . .	. . . .	3	1.03	. . . . . .	. . . . . .
	Isoetes saccharata.	. . . .	2	1.33	. . . . . .	. . . . . .
Weighted mean.	. . . .	. . . .	. .	1.00	. . . . . .	0.054

the plant wilts, the soil farthest from the roots contains more water than the soil immediately surrounding the roots. Consequently, the determination of the moisture content of the whole soil mass at the time of wilting gives too high a value for the wilting coefficient. Aside from the *Colocasia*, a variety of corn gave the highest relative wilting coefficient, namely, 1.06. The several varieties of corn differed slightly, the lowest value being given by Boone County white, a variety native to wet regions. Mexican and Indian varieties, natives of dry regions, gave no evidence of being able to reduce the soil moisture content lower than other varieties. Only slight differences were found in the relative wilting coefficient in the different varieties of sorghum, a crop extensively grown in semi-arid regions. The relative wilting coefficient of two of the varieties tested was 0.94, indicating that these varieties were capable of reducing the moisture content of the soil somewhat below the point reached by corn at the time of wilting. The difference in the wilting coefficient of the varieties of the small-grain crops, millet, wheat, oats, and barley, is slight, the extreme range for the four crops being from 0.95 to 1.03. The value of the wilting coefficient obtained for rye was 0.94 and for Japan rice 0.92. The low value found for the latter plant is of special interest in view of the fact that it is generally considered necessary to keep rice fields flooded during the greater part of the growing season.

The different grasses, most of which are natives of the Great Plains of the United States, gave ratios differing only slightly from each other and from the small grains. Most of the legumes, on the other hand, and certain of the coarse-rooted plants of the Great Plains, gave slightly higher values for the relative wilting coefficient. These high values, we believe, are to be attributed to imperfect root distribution rather than to any inherent inability of these plants to reduce the soil moisture content to the point reached by other plants.

The miscellaneous plants upon which only a few determinations have been made are grouped in the last part of the table as hydrophytes, mesophytes, and xerophytes. The water plants gave a mean wilting coefficient slightly higher than the other groups, due to the presence in this group of *Isoetes*, submerged plants of which

were taken from the water and grown in the air without being permitted to develop new leaves. This plant also had a poor root distribution. If we except *Isoetes*, the other hydrophytes give a mean wilting coefficient identical with that of the mesophytes. The xerophytes tested gave a mean ratio intermediate between the hydrophytes and mesophytes. This would indicate that plants native to dry regions are unable to reduce the water content of the soil to a lower point than is reached by other plants at the time of wilting.

TABLE II

THE RELATIVE WILTING COEFFICIENT FOR DIFFERENT PLANTS

Plant	No. of observations	Mean ratio	Probable error	
			Of mean ratio	Of single ratio
Zea	75	1.03	0.003	0.042
Andropogon	66	0.98	0.008	0.062
Chaetochloa italica	48	0.97	0.006	0.035
Triticum	653	0.994	0.002	0.049
Avena	46	0.995	0.007	0.047
Hordeum	60	0.97	0.006	0.047
Secale	19	0.94	0.011	0.049
Oryza	21	0.94	0.012	0.054
Gramineae	77	0.97	0.005	0.040
Leguminosae	138	1.01	0.005	0.059
Cucurbitaceae	17	0.99	0.016	0.068
Lycopersicon	20	1.06	0.009	0.040
Colocasia	19	1.13	0.005	0.066
Hydrophytes	8	1.10	0.037	0.105
Mesophytes	35	1.02	0.010	0.058
Xerophytes	16	1.06	0.008	0.032
Total number of observations	1,318	.....	.....	.....
Weighted mean	.....	1.00	.....	.....

The results of the different crops have been summarized in table II without reference to varieties. Reference to the table will show that only slight differences exist among the various crops in their ability to reduce the soil moisture content before wilting occurs. Sorghum, millet, wheat, oats, barley, and the grasses are practically the same. Rye and rice appear to be a little lower than the mean, corn and the legumes slightly higher.

U.S. Department of Agriculture
Bureau of Plant Industry
Washington, D.C.

ALTERNATION OF GENERATIONS IN CERTAIN FLORIDEAE

I. F. LEWIS

Cytological observations on *Polysiphonia* by YAMANOUCHI[1], *Griffithsia* by myself,[2] and *Delesseria* by SVEDELIUS,[3] render it probable that in these genera at least, and presumably in all Florideae in which tetraspores and sexual organs are regularly borne on separate individuals, there exists an alternation of sexual and asexual plants, the carpospores giving rise on germination to asexual, and the tetraspores to sexual individuals. For the past two summers at Wood's Hole I have been engaged in putting this matter to the proof by actual cultivation of the sporelings to maturity. This would seem to be a simple matter, but experience has shown me, as it has many others, that the range of physiological tolerance of these forms is extremely small. Temperature, light, and other less easily regulated factors may vary only within very narrow limits. All attempts to carry sporelings to maturity in the laboratory having failed, a plan was adopted similar to that employed by HOYT[4] in solving an analogous problem in Dictyota.

The method consisted in sowing spores on oyster shells, and transferring these to the open water after the sporelings had become firmly attached. The shells were soaked for at least 24 hours in fresh water and then scraped clean with a brush. Three small holes were made in each to facilitate its subsequent attachment. The shells so prepared were placed in deep glass vessels in filtered sea water. Fruiting algae of the desired species were then washed in running water for a few minutes, and placed in the vessels over

[1] YAMANOUCHI, S., The life history of *Polysiphonia*. BOT. GAZ. **42**:401–449. 1906.

[2] LEWIS, I. F., The life history of *Griffithsia Bornetiana*. Ann. Botany **23**:639–690. 1909.

[3] SVEDELIUS, N., Ueber den Generationswechsel bei *Delesseria sanguinea*. Svensk Botanisk Tidskrift **5**:260–324. 1911.

[4] HOYT, W. D., Alternation of generations and sexuality in *Dictyota dichotoma*. BOT. GAZ. **49**:55–57. 1910.

the shells. This was usually done in the afternoon, and the algae taken out the next morning. The spores of most species were shed in abundance, the resulting sporelings becoming attached almost immediately. At first the dishes were kept in the laboratory till the sporelings had become about 2 mm. long, and the shells were then transferred to the waters of Vineyard Sound. In such cases, however, the sudden change of environment exerted a deleterious effect on growth. For this reason, in all the later experiments the shells were transferred on the second day after the spores were shed. This was found to allow ample time for firm attachment of the sporelings. Each shell, before being "planted," was minutely inspected with a lens, and only those were used which showed a good uniform "stand" of sporelings without visible contamination from the spores of other species. Close inspection was especially necessary in the case of *Griffithsia* and various species of the Rhodomelaceae, on account of the frequency in these forms of vegetative multiplication from the broken off tips of the filaments. No attempt to thin out the sporelings was made.

Tarred cord, first soaked for some months in salt water to extract the soluble matter in the tar, was used for attaching the shells. A sort of ladder was made by having two parallel cords about 6 inches apart, to which shells were tied by cord running from the three holes mentioned. A ladder prepared in this way was either stretched horizontally between two supports, such as stakes firmly driven into the bottom or allowed to hang vertically from a pile. In the latter case the parallel cords were weighted at the bottom, to prevent the ladder from becoming tangled by the tidal currents. The latter method proved more satisfactory, as in this way, by having a series of shells bearing sporelings of one species, the optimum depth for the growth of that species could be readily determined. This was found to vary with the species employed, but in general it was about 2–3 feet below mean low water.

Plantations were made at Spindle Ledge, on the piles of the Government Wharf at Little Harbor, and on the piles at the end of the Fay Wharf. The best results were obtained at the last mentioned locality. The water here is very deep, th

piles standing in the edge of the main channel. The rapid flow of the tides, and perhaps other factors, seem to prevent the attachment of spores, so that the algal flora at this point is quite scanty. This was found to be of importance for the reason that shells placed here showed almost no contamination from unknown sources, while at the other localities foreign spores settled and grew so abundantly and luxuriantly that the planted spores were overcrowded. Furthermore, at Spindle Ledge a considerable mass of drift, consisting for the most part of tangled mats of *Ectocarpus*, caught on the cords and prevented the development of the algae sown. In all, about 125 shells were planted.

The plantations were all made in July. The shells were left in the water 21–45 days. It was found, however, that in those species in which definite results were obtained, little if any growth took place after August 15. On all shells taken up as late as September 1, the algae were found to be disintegrating. After being collected, each shell was examined with the greatest care. Every visible growth, animal or plant, was scraped off and minutely inspected under the compound microscope. In this way possibility of error of observation was eliminated as far as could be done. In the course of the microscopic examinations, many observations were recorded as to the rate of growth of various species, the relative abundance of spores at different localities, and other matters not included within the scope of the present paper.

The following species were used: *Spermothamnion Turneri* Aresch., *Callithamnion Baileyi* Harv., *Griffithsia Bornetiana* Farlow, *Ceramium rubrum* Ag., *Ceramium fastigiatum* Harv., *Cystoclonium purpurascens* Kütz., *Chondrus crispus* (L.) Stack., *Lomentaria uncinata* Menegh., *Champia parvula* (Ag.) Harv., *Agardhiella tenera* (J. Ag.) Schmitz, *Grinnellia americana* Harv., *Gracilaria multipartita* J. Ag., *Chondria tenuissima* (Ag.) Harv., *C. dasyphila* (Ag.) Harv., *Polysiphonia fibrillosa* Grev., *P. violacea* Grev., *Dasya elegans* Ag. (17 species). Of these, the majority proved to be unsuitable, definitive results being obtained only with *Polysiphonia violacea*, *Griffithsia*, and *Dasya*. The failure to obtain results with some was due to lack of proper environment, since no shells were planted in deep water where such forms as *Gracilaria*, *Spermotham-*

nion, and *Cystoclonium* are found. In other cases, as *Chondrus* and *Agardhiella*, growth of the sporelings was so slow that they became covered and killed by the growth of exotic spores. In still others, the sporelings failed to become established, even the short time in which they were under laboratory conditions being sufficient to cause them to cease growing. Strange to say, some of these, as *Ceramium rubrum* and *Chondria tenuissima*, seem to be quite hardy, and are abundant and luxuriant in situations similar to those in which the shells were planted. Still others, including *Champia* and *Lomentaria*, were early discarded because of the frequency with which these species establish themselves on any suitable solid support.

Record of experiments

I. *Agardhiella tenera*.—Tetraspores and carpospores sown July 18, 1910, transferred to Spindle Ledge July 19. Shells collected August 10, and found to be much overgrown with foreign algae. Search revealed hundreds of small sterile *Agardhiella* plants, of which the average length was 0.5 mm. Some were of good color and apparently vigorous, but the great majority had ceased growing and were beginning to become discolored. The most interesting point about this culture was the fact that the sporelings from carpospores and tetraspores were of exactly the same size and conformation.

II. *Grinnellia americana*.—Treatment like that of *Agardhiella*. Hundreds of sterile specimens were found, 3–4 mm. long, vigorous and of good color. The fact that the amount of growth in 24 days at the height of the growing season was so slight would seem to indicate that this species, like the preceding one, is biennial, the sporelings of one summer reaching maturity the next year.

III. *Polysiphonia violacea*.—Tetraspores and carpospores sown July 18, 1911, transferred to piles at end of Fay Wharf July 20, collected August 14. The shells sown with tetraspores were accidentally destroyed before being collected. On examination, the shells sown with carpospores were found to be pretty thickly overgrown with *Polysiphonia variegata*, mostly sexual. Scattered among these plants, however, were 29 individuals of *P. violacea*, varying in length from 1.0 to 3.1 cm. The color of all was darker

than usual, and the plants seemed to be stunted. The main branches ended much more abruptly than is common in this species, and the development of hairs was sparse. The apices, however, were normal, and the plants still growing. All the smaller individuals, 23 in number, were found to be sterile, but 6, comprising the largest specimens, bore tetraspores normally and abundantly. On neighboring shells, which were examined very carefully as controls, no *P. violacea* was found. The only contaminating species were *P. variegata* in great numbers, *Champia parvula* (averaging 3 individuals to each shell), and *Dasya elegans* (2 per shell). It may be remarked parenthetically that *P. violacea* and *P. variegata* are species that are quite distinct, and easily and surely recognizable.

In this experiment, carpospores were found to produce tetrasporic plants, and no sexual individuals.

IV. *Griffithsia Bornetiana.*—Carpospores sown July 18, 1910, transferred to Spindle Ledge July 19, shells collected August 12. The stand of *Griffithsia* was found to be unusually good, the shells resembling miniature lawns on which *Griffithsia* was the grass. The individuals were so closely appressed and interwoven at the base that it was impossible to ascertain the exact number, which must, however, have reached into the hundreds. The largest were about 2 cm. long, a size at which sexual individuals fruit fairly abundantly, but all were sterile.

Tetraspores sown July 2, transferred to Spindle Ledge July 18, 1910, shells collected August 10. The maximum length attained was 1.5 cm., and the average 0.75 cm. Numerous very small sterile individuals were found. Of those specimens which had attained a length of 1.0 cm., 23 showed developing sexual organs, and 7 were sterile. Of the sexual plants, 12 were male and 11 female. Neighboring shells used as controls were destitute of *Griffithsia*. The results of this experiment were confirmed by cultures made in 1911. Tetraspores from a single plant were sown July 15, transferred to piles at Little Harbor July 18, shells collected August 14. The largest individuals were stocky, bushy plants 3 cm. long, and all were well developed, there being little crowding with the resulting production of dwarfed specimens. From one shell 45 individuals were obtained, of which 8 were sterile,

20 male, and 17 female. In the female plants ripe carpospores were being produced at the time of collection. Neighboring shells, as before, showed no *Griffithsia*. The contaminating species were *Champia parvula* (5 per shell), *Lomentaria uncinata* (4), *Grinnellia americana* (1), and *Polysiphonia variegata* (1).

A very interesting feature of this culture was the occurrence of two large apparently hermaphroditic individuals. In each case, close inspection revealed the fact that the apparently single individual was really a complex of four plants in intimate contact at the base. The rhizoidal filaments were interwoven somewhat, but could be separated with needles. Of the four, two were male, two female. The four spores from one tetrasporangium of *Griffithsia* frequently remain in contact after being shed, so that four spores may often be seen lying in immediate proximity, all derived from the same sporangium. In the cases mentioned, it seems as if this must have happened, and the four individuals composing the single compound plant have been derived from the four spores of a single sporangium. Further experiments will be made to settle this point.

V. *Dasya elegans.*—Carpospores could not be obtained early enough in the season to give positive results. Tetraspores sown July 18, 1911, transferred to Fay Wharf July 19, shells collected August 14. The stand of *Dasya* was quite good, but the individuals remained clearly separate, not running together at the base as in the case of *Griffithsia*. The largest specimens measured 4.5 cm. long, with 6 or 8 side branches from the main stem. The average length was 2 cm. Of the largest and best developed specimens, measuring more than 3 cm. in length, 6 were female, 7 male, and 1 sterile. Of the total number of individuals, 139 were sterile, 143 male, and 6 female. In interpreting this result, it is necessary to bear in mind that antheridia may develop when the plants are quite small (0.5 cm. long or in exceptional cases even less), while procarps do not begin to form in individuals less than about 3 cm. long. On control shells no *Dasya* developed. The most abundant contaminating species was *Polysiphonia variegata*, while *Champia parvula*, *Ceramium rubrum*, *Chondria tenuissima*, and *C. dasyphila*, along with *Enteromorpha* sp., occurred rarely.

What may be called the reciprocal cultivation of a single species has not yet been attended with success. It is more difficult to raise carposporelings to maturity than tetrasporelings, for the reason that tetrasporic plants are usually late in fruiting, while sexual individuals may be expected to produce reproductive bodies in 3–5 weeks. The experiments in their present status show, however, that in *Griffithsia* and *Dasya* the tetraspores actually do produce sexual plants, and only these, and that in *Polysiphonia violacea* carpospores produce only tetrasporic plants. The results of the experiments go to show, therefore, that the conclusions drawn from cytological evidence are valid, and that alternation of sexual and tetrasporic plants in the Florideae is now an observed fact.

In conclusion, it is a pleasure to acknowledge my indebtedness to the friends who have assisted me in various ways in the progress of this work, particularly Professor Geo. T. Moore, Dr. Ernst A. Bessey, Mr. H. Wasteneys, and the officers of the Supply Department of the Marine Biological Laboratory.

Summary

1. There is no evidence that the double number of chromosomes in the carpospores imparts greater vigor of growth as compared with the single number of the tetraspores.

2. From the carpospores of *Polysiphonia violacea* 6 tetrasporic plants were obtained, and none sexual.

3. From the tetraspores of *Griffithsia Borneliana* 60 sexual individuals were produced, and none tetrasporic.

4. From the tetraspores of *Dasya elegans* 149 sexual plants were secured, and none tetrasporic.

5. Tetraspores from a single individual produced male and female plants in approximately equal numbers in *Griffithsia*. The preponderance of males in *Dasya* is explained by the early fruiting of these as compared with the females.

Randolph-Macon College,
Ashland, Virginia

A STUDY OF HYBRIDS BETWEEN NICOTIANA BIGELOVII AND N. QUADRIVALVIS[1]

E. M. EAST

(WITH FOUR FIGURES)

The genus *Nicotiana* was divided by G. DON into four sections: TABACUM, RUSTICA, PETUNIODES, and POLIDICLIA. This classification has been followed in all *Nicotiana* monographs down to the present day, although several species have been shifted back and forth. The section POLIDICLIA is based upon *Nicotiana quadrivalvis* Pursh (Lehm. *Gen. Nic. Hist. pl. 4*) and its variety *multivalvis* Gray (*Syn. Fl. N. Amer.* **2**[1]: p. 253). (See COMES' *Monographie du genre Nicotiana.* Naples. 1899, p. 54.) The experiments on *N. Bigelovii* Watson and *N. quadrivalvis* Pursh reported in this paper show that such a section is unwarranted.

The writer began an extended series of genetic investigations upon the species of the genus *Nicotiana* in 1907 at the Connecticut Agricultural Experiment Station. Seed of several species was very generously given by Professor O. COMES of Naples, Italy, through Dr. D. G. FAIRCHILD of the United States Department of Agriculture; by Dr. A. SPLENDORE of Scafati, Italy; and by Professor W. A. SETCHELL[2] of the University of California. The source of the seed from Italy is unknown to me, but several of the species obtained from Professor SETCHELL were only one or two generations removed from the wild. The following description of *N. quadrivalvis* Pursh is taken from Gray's *Synoptical flora of North America.*

N. QUADRIVALVIS Pursh. A foot high, rather stout, more or less viscid pubescent, low-branching: leaves oblong or the uppermost lanceolate and the lower ovate-lanceolate, acute at both ends, mostly sessile (3–5 in. long); the

---

[1] Contribution from the Laboratory of Genetics, Bussey Institution of Harvard University. No. 14.

[2] I had the pleasure of describing some of my experiments with *Nicotiana* hybrids to Professor SETCHELL, during his visit to Boston last winter. He said at that time that he had reached conclusions similar to mine in regard to *N. Bigelovii* and *N. quadrivalvis*, although what experiments he has made I am unable to state.

lowest larger and petioled: flowers few; calyx teeth much shorter than the tube, about equalling the 4-celled (or sometimes 3-celled?) capsule: tube of the corolla barely an inch long, the 5-lobed limb an inch and a half or more in diameter; its lobes ovate and obtusish, veiny.

Oregon, and cultivated by the Indians from Oregon to Missouri; their most prized tobacco plant. Perhaps a derivative of the preceding species.[3]

Three sets of seed, purporting to be this species, two from Italy and one from California, were grown. The plants obtained were

FIG. 1.—At left, *Nicotiana quadrivalvis* Pursh; at right, *N. Bigelovii* Watson; young plants.

alike in every detail within the limits of fluctuating variation. One selection has bred true for four generations. They differed from the above description in only one character. The lower leaves could hardly be called petioled, although they tapered almost to a petiole. The plants when grown in a normal fertile soil always had a large number of capsules with four cells. There were individual capsules, however, with three and sometimes even two cells on the same plants. This feature is evidently a physiological variation, for when grown in small pots in the greenhouse

[3] This statement, overlooked by me until the conclusion of the experiments, refers to *N. Bigelovii*.

and partially starved, the percentage of two-celled and three-celled capsules is much increased. The progeny of the starved plants gave only normal plants.

GRAY'S description of *N. Bigelovii* Watson is as follows:

N. BIGELOVII Watson. A foot or two high: leaves oblong-lanceolate, sessile or nearly so; the lower (5–7 in. long) with tapering base; the upper (3 to 4½ in. long) more acuminate, with either acute or some with broader and partly clasping base; inflorescence loosely racemiform, with all the upper flowers bractless: calyx teeth unequal, linear-subulate, about equalling the tube, surpassing the capsule: tube of the corolla 1½ to 2 in. long, narrow, with a gradually expanded throat; the 5-angulate-lobed limb 12–18 lines in diameter.

FIG. 2.—At left, *Nicotiana quadrivalvis* Pursh; at right, *N. Bigelovii* var. *quadrivalvis;* mature plants.

Seed from Italy and from California gave plants agreeing perfectly with this description. What was not so noticeable in the published descriptions of the two species was the remarkable similarity of living plants of the two species *N. Bigelovii* and *N. quadrivalvis*. The latter differs from the former only in its smaller size and the number of cells in the capsule. Even the viscid odor, which is stronger than in other species of the genus with which I am familiar, is the same in both. It naturally occurred to me that they might both be the same species, a thought simply a little more radical than the one that had already occurred to GRAY.

The species were crossed, therefore, and gave perfectly fertile hybrids intermediate in character, with partial dominance of the

four-celled capsule. Unfortunately the cross between the normal two-celled *N. Bigelovii* and *N. quadrivalvis* has been lost. It is interesting from the standpoint of the transmission of that character, and will be remade.

The similarity of the two plants and the fact that they give a cross that is fertile in the F_1 generation is sufficient evidence to convince me that *N. quadrivalvis* Pursh is really *N. Bigelovii* var. *quadrivalvis*. There is further evidence in the fact that *N. Bigelovii* has produced a *quadrivalvis* variety while under observation.

FIG. 3.—At left, *Nicotiana Bigelovii* var. *quadrivalvis*; at right, *N. quadrivalvis* Pursh; in center, F_1 generation of reciprocal crosses.

Several plants from the different selections of *N. Bigelovii* with a single capsule having three cells were observed. Seeds from these plants were selected with the object of producing a race having three-celled capsules. Selection had absolutely no effect. Among the progeny an occasional three-celled capsule was found, but the percentage could not be increased. In this strain of *N. Bigelovii* there was evidently no ability to transmit the three-celled character. It simply gave an occasional zygotic variation of this kind, just as do many other species of *Nicotiana*.

On the other hand, several other plants, typically *N. Bigelovii* in size, produced several three-celled capsules. It is quite probable that they were all progeny of one plant of the preceding generation. One of these plants was selfed and the resulting seed planted on

rich ground the following year.[4] Each plant among the progeny had numerous three-celled capsules, together with occasional two-celled and four-celled capsules. For two generations the strain has bred true to this condition. The only other abnormality observed is the occurrence of a greater number of flowers with six sepals and six petals than is common in the normal *N. Bigelovii* or the *N. quadrivalvis.* About 1 per cent of the flowers from the normal species have the extra petal and sepal, but on individual plants in

FIG. 4.—At left, *Nicotiana Bigelovii* var. *quadrivalvis;* at right, *N. quadrivalvis* Pursh, in center, F_1 generation of cross.

the aberrant strain of *N. Bigelovii* from 2 to 5 per cent of the flowers vary in this manner.

The aberrant *N. Bigelovii* was crossed reciprocally with *N. quadrivalvis.* The F_1 plants were alike in each case. They were intermediate in stature and in size of flower. The earlier capsules were four-celled; later in the season both three cells and two cells were produced. The F_1 plants were fully as fertile as the parent species. Each plant produced hundreds of well filled capsules.

[4] Seeds are always started in sterilized soil and seedlings set in the open.

One plant each from the cross and its reciprocal were selfed. About 70 plants were grown from each mother plant. No difference was noticed in the two F_2 generations. The entire lot can therefore be considered together. The plants varied in height from one foot to two feet. The flowers were in general intermediate in size, but varied to the extremes that characterize each parent. No plants having only two-celled capsules were found; 71 had a large number of four-celled capsules; 40 had only a few four-celled capsules; while 19 had no four-celled capsules. Every plant had large numbers of three-celled and two-celled capsules, whether or not four-celled capsules were present.

Summary

1. Two elementary species of *N. Bigelovii* Pursh have been found. In one the capsules are two-celled and selection of individuals having an occasional three-celled capsule does not increase the tendency; in the other the tendency to have a greater number of cells than two in the capsule is always transmitted.

2. *N. quadrivalvis* Pursh and normal *N. Bigelovii* Watson are alike in all specific characters except the number of cells in the capsule, and since they give fertile hybrids when crossed it is thought that *N. Bigelovii* gave rise to *N. quadrivalvis*.

3. It is proposed that the section POLIDICLIA in the genus *Nicotiana* be dropped, and *N. quadrivalvis* Pursh be called *N. Bigelovii* var. *quadrivalvis*.

HARVARD UNIVERSITY.

CURRENT LITERATURE

BOOK REVIEWS

Textbooks of plant physiology

The third edition of GREEN'S *Vegetable physiology*[1] is a newly printed, if not a newly written, book. The first impression to be gained by one who is already familiar with the second edition is that the present volume is a better piece of book manufacture than the older one; especially are the figures brought out much more clearly on the new paper.

A careful comparison of the second and third editions brings out the fact that the essentials of the book remain unchanged in the latter. A good many changes which comprise but a few words are to be noted; some statements are strengthened or weakened or dropped out; some records of discoveries or suggested hypotheses which were originally expressed in the present perfect tense are now thrown into the past; words and phrases are added or removed in the interest of clearness or of elegance; and the paragraphing of the older matter has been here and there improved. A number of new paragraphs have been inserted and some old ones have been supplemented; a few have been totally rewritten. In but a very few cases has the arrangement of the paragraphs been radically altered. A very few figures have been improved by redrawing. While the reviewer is convinced that practically all the changes made are in the direction of the improvement of an already very readable and scholarly treatise, he is distinctly of the opinion that these changes are generally unimportant, and that those who know the second edition practically know also the third.

In general, the chemical considerations seem better framed than the physical ones; the former are often excellent, while the latter are more frequently slighted or seemingly treated in a merely perfunctory way. The time-worn logical fallacy, for example, of supposing that turgidity of cells is produced by hydrostatic pressure (a pressure exerted by *water* to distend a membrane *permeable to water*, through which, indeed, the very water to produce this outward pressure is supposed to have just passed!) is here met with anew.

Even by assuming the position that the *results* of transpiration are the *reasons* for its occurrence, the reviewer is unable to follow the argument of p. 82, wherein it is implied that growth is slow in cacti, etc., because the transpiration rate is low. The proposition appears to be that much water must be

[1] GREEN, J. REYNOLDS, An introduction to vegetable physiology. 3d ed. pp. xviii+470. *figs. 182*. Philadelphia: P. Blakiston's Son & Co. 1911.

transpired in order to bring much saline material into the plant, that large amounts of salts are necessary to rapid and vigorous growth, and hence that with low rate of water loss we must expect slow growth or none at all. After all, in spite of the cuticularization and the relatively small surface exposed by cacti, it is probable that such plants, in their desert habitat, transpire as much per unit of volume as do many very leafy and luxuriantly growing forms of the rainy tropical forest. Furthermore, the growth of the desert cactus occurs in the moister season of the year, exactly at the time when its transpiration is least, or at any rate when it *would be least*, were it not for the slightly cuticularized surfaces of the new growth.

The advance of plant physiology away from the older anthropomorphic interpretation, which seems to characterize the opening of the present century, and the clear indication thus given that we shall ultimately have a purely rational physiology, leads the reviewer to deplore the fact that a text otherwise so perfect and so teachable should be so imbued with the old teleological view of natural phenomena. Of course, it is to be recognized that our science has not, in general, advanced far toward the elimination of this form of superstition; indeed, the author of the volume before us is perhaps with the majority of biologists when he shows that his is a teleological view of plant phenomena. Those teachers who wish to avoid as long as possible the complete reduction of biology to the uncolored and impersonal status of the other physical sciences will find here a textbook which will meet their requirements. For, aside from this imaginative coloring, the book is as nearly suited to its purpose as a book is apt to be. But it should be realized clearly that this is an account of physiological processes from the standpoint of the "benefit" or "advantage" or "purpose" or "aim" of the plant in allowing its various activities to be controlled by physical and chemical conditions. From p. 377 we select: "In considering broadly the result of stimulation we must notice at the outset that it provokes a *purposeful* response. The living substance appears to have a definite aim"; etc. The italics are the author's. Again, on the next page occurs, "Less conspicuously purposeful are those changes in metabolism which are brought about with the supply of food or oxygen, but even here evidence of purpose can be found if sought for."

Our conclusion with reference to the work before us is that while it was for a decade the most satisfactory English elementary presentation of its subject, the advance of the science has made it unsuitable for class work, unless the instructor wishes, indeed, to emphasize the teleological aspect of physiology.

The day of a true science of physiology seems to be at hand, judging from the increased activity in the general phase of this subject witnessed by the last few years. By a true science is meant here a physiology which belongs specifically neither to botany nor to zoology, a science of the phenomena of life, wherever these phenomena may occur. Those who have drawn inspiration and breadth of view from VERWORN'S *Allgemeine Physiologie* will welcome

a volume which has just appeared from the pen of A. PÜTTER,[2] a student of VERWORN'S, associated with him at Bonn. PÜTTER'S book will be especially interesting to physiologists who have entered the science through studies with plants, partly because the author states in his preface that PFEFFER'S *Pflanzenphysiologie* "exerted the most lasting influence upon his scientific development," and still more because of the freedom and general efficiency with which he incorporated numerous facts and principles of plant physiology in his treatise. There has not appeared previously a book of readable size, which is so truly a comparative physiology as is the present volume. About one-fourth of the figures are taken from plant material.

Having announced in his introduction that the study of all life-processes is the field of physiology, and that an understanding of these processes is to be obtained only by *comparison*, the emphasis being laid upon points of similarity in various organisms rather than upon those of difference, PÜTTER proceeds to discuss, with many citations of the more recent literature, the following nine topics, which form the chapter headings of the book before us (i) The substratum of the life processes, (ii) Metabolism, (iii) Nutrition, (iv) Exchange of material, (v) Conditions of life, (vi) Energy transformations, (vii) Responses to stimuli, (viii) Organs of perception, (ix) Nervous system.

In the first chapter, under "The physical constitution of living substance," the author gives a brief but clear presentation of these aspects of colloidal chemistry, an understanding of which is most necessary to physiological thinking. Under "The constituents of organisms," he discusses water and the various groups of chemical compounds that find a place in living beings. The point is well made that water is to be considered as fundamental to all life, and it is shown that, in general, the water content of the active parts of plants and animals may be taken to be about the same.

In the following chapters, of which spatial limitations prevent any consideration here, the author's treatment of the various processes and activities of organisms is always carried out from the standpoint of physics and chemistry, at least the methods of these sciences in attacking a problem are here always evident. Anthropomorphic terms and ways of viewing life-processes are rarely admitted and only with proper logical consideration. The aim is always to arrive as nearly as possible at the underlying principles according to which the different processes go forward, to bring out the cause of each effect and the quantitative relations which exist between these. The book emphasizes in a gratifying and encouraging way the considerable degree to which the simpler mathematical expressions of physical science are already being incorporated in physiological reasoning.

While every reader will find certain points wherein he and the author may disagree, we have found the volume exceptionally logical in its generalizations

---

[2] PÜTTER, A., Vergleichende Physiologie. pp. viii+721. *figs. 174.* Jena: G. Fischer. 1911.

and exceptionally open-minded in the matter of the many moot questions which so largely make up our present science. What might be considered as errors or inadequacies of treatment are no doubt largely explainable on grounds of lack of space for a full consideration of the questions involved. It is not likely that the book will lead any serious worker far astray.—B. E. LIVINGSTON.

Manual of carboniferous plants

The work, of which Doctor JONGMANS has published the first part under the title cited,[3] is destined to constitute a manual of the carboniferous plants of western Europe. As may be inferred, it is intended for the use of students and paleontologists who have under examination the ordinary impressions and carbonized fragments which constitute over 99 per cent of the material representing the carboniferous floras. The treatment is adapted primarily, therefore, to the identification of such plant fragments. Accordingly the histologist, looking for descriptions or illustrations of the microscopical structure of carboniferous plants, will not find much information of that kind in the work, or at least in its first part. As a matter of fact, there are in the Paleozoic comparatively few plant genera the microscopical anatomy of which is known, because in most formations the geologist very rarely encounters petrified material admitting of histological comparison. Such material, when it is found, is almost invariably limited to restricted areas, as well as very distant stratigraphic horizons. From the stratigraphic standpoint petrified plant fragments, which are apt to lack superficial characters, are of relatively little value.

The paleobotanical matter in the work is arranged to serve the purpose of greatest practical utility. The pteridophytes are grouped in (1) Equisetales, (2) Sphenòphyllales, (3) Lycopodiales, and (4) Filicales, to which, as an appendix, is added (5) Cycadofilices or the Pteridospermae. The first volume, embracing 482 pages, ends with the Sphenophyllales. Each group, family, and genus is briefly but lucidly defined, the descriptions and differentiations being often graphic in their simplicity and effectiveness. In most cases where the genus or subgenus includes half a dozen or more species, carefully prepared and most useful keys are introduced to aid in the identification of the fossils. Most of the species are also illustrated to show their diagnostic features, and the pains and good judgment which the author has shown in the choice of his illustrations, a large number of which represent type specimens, contributes materially to the value and importance of the work. All these features combine to make it a reference work for the use of systematic or stratigraphic paleobotanists.

[3] JONGMANS, W. J., Anleitung zur Bestimmung der Karbonpflanzen West Europas mit besonderer Berücksichtigung der in den Niederlanden und den benachbarten Ländern gefundenen oder noch zu Edwartenden Arten. Band I. Thallophytae, Equisetales, Sphenophyllales. 482 pp. *figs. 390*. 's Gravenhage: Mededeelingen van de Rijksopsporing van Delfstoffen. 1911.

In his point of view JONGMANS is generally fairly conservative. His species are for the most part clearly delineated, as shown by the synonomy, though in some cases plants have been included under a single name, which in the judgment of the reviewer, should be maintained separately. An example is *Calamites inornatus* Dawson, here included under *Asterocalamites scrobiculatus*, but really a *Pseudobornia*. On the other hand, there are very many instances of wise and careful reconstruction and correlation. It is assumed that the parts yet to be printed will, like the one in hand, be accompanied by bibliographies and complete indexes, which will aid in making the book the most useful, I may say indispensable, work that has yet been published for the systematic identification of ordinary carboniferous plants.—DAVID WHITE.

Poisonous plants

PROFESSOR PAMMEL has published a *Manual of poisonous plants*[4] whose bulk is a surprise. The reviewer did not imagine that there were so many poisonous plants in the whole world, and the author has restricted himself to "chiefly eastern North America." An explanation is found in the broad interpretation of the subject, for the book includes "all plants that are injurious, although many of these are not known to produce poisons, some even being most useful economic plants and yet injurious to some people."

After the surprise of bulk has subsided, the appalling amount of bibliographical work becomes impressive. At the end of the volume is a bibliography of poisonous plants, a bibliography that must have been traversed more or less completely, and it contains 1237 titles (50 pp.). In addition to this, there is "a catalogue of the poisonous plants of the world" (59 pp.), and also a very complete index (59 pp.).

Part I (150 pp.) includes the presentation of the subject from the standpoint of the poisons, as the titles of the 15 chapters will indicate: Poisons and statistics on poisons; Bacterial poisons; Dermatitis; Forage poisoning, ergotism, and aspergillosis; Poisoning from fungi; Poisoning from other plants—equisetosis, locoism, and lupinosis; Delphinosis, lathyrismus (lathyrism), aconitism, veratrism, Umbelliferae, Conium, Cicuta; Fish and arrow poisons, hydrocyanic poisoning, toxalbumins; Poisoning from opium; Solanaceae and plants that contain saponins; Poisoning from flowers and from honey, mechanical injuries; Classification of poisons, symptoms, and antidotes; Production of poison in plants; Algae in water supplies; Catalogue of the more important poisonous plants of the United States and Canada; Chemistry of alkaloids, glucosides, etc.

Part II (652 pp.) is a descriptive manual, with keys, numerous illustrations, and all the data necessary for determination. The sequence used is that of

[4] PAMMEL, L. H., A manual of poisonous plants; chiefly of eastern North America, with brief notes on economic and medicinal plants, and numerous illustrations. 8vo. pp. xiv+977. *pls. 17. figs. 458.* Cedar Rapids (Ia.): The Torch Press. 1911.

ENGLER and PRANTL'S *Die natürlichen Pflanzenfamilien*, beginning, therefore, with slime molds and ending with thistles; and with each plant there is given the recorded facts as to its injurious effects, and also such medicinal qualities as seem important.

The volume is a great compendium of well-organized information in reference to a subject that has been attracting a good deal of attention recently at national and state agricultural experiment stations in connection with plants injurious to live stock, but of course its scope extends far beyond that special interest. The author is to be congratulated upon the completion of a work that must have involved an unusual amount of patient toil and organizing power.—J. M. C.

Subantarctic New Zealand

The Philosophical Institute of Canterbury, New Zealand, has published in cooperation with the government a most admirable work on the geology, botany, and zoology of the Subantarctic Islands of New Zealand.[5] In the introduction there is given by the editor, Dr. CHILTON, an interesting account of the scientific investigation of these islands; this part contains a number of excellent photographic reproductions of characteristic landscapes. There are six papers dealing with the botany of the islands, one of which is by PETRIE on the grasses (pp. 472–481), one by LAING on the marine algae (pp. 493–527), and one by various collaborators, giving a list of the fungi and bryophytes.

Three botanical papers are of somewhat wider interest and may be noticed briefly. CHEESEMAN gives a somewhat detailed account of the systematic botany (pp. 389–471). This paper includes a historical account of the botanical exploration of the islands, an annotated list of the vascular plants, a tabular view of their distribution in the individual islands and elsewhere in the world, and an interesting concluding part on the affinities of the flora. The flora consists largely of a New Zealand element, representing probably recent immigrations; there is also an interesting Fuegian element, as well as an endemic element. The idea of recent and extensive land connections is not favored.

COCKAYNE gives in his usual satisfactory style an account of the ecological botany of the islands. The leading physiognomic plants are briefly treated, after which the ecological factors are considered, wind being regarded as the most important single factor. Then follows an account of the special ecology of the plants. The body of the paper presents the plant formations, which are more numerous than one might expect to be the case. On the Snares one of the most important formations is the *Olearia Lyallii* scrubby forest. On the Auckland Islands occurs the rata forest, dominated by *Metrosideros lucida*, and known through previous papers by COCKAYNE; this formation tapers off

[5] CHILTON, CHARLES, with various collaborators, The Subantarctic Islands of New Zealand. pp. 848. *1 map. pls. 25.* numerous figs. Wellington, N.Z.: Philosophical Institute of Canterbury. 1910.

into a mountain scrub, consisting chiefly of stunted rata. The Auckland Islands have also extensive meadows and bogs. The paper closes with an account of the important influence played by animals upon the vegetation.

The plant formations of Campbell Island are described by R. M. LAING. This island contains no trees, the tallest vegetation being the *Dracophyllum* scrub; the treelessness is ascribed to the violent westerly gales. Apart from the scrub, Campbell Island has interesting tussock meadows. Some of the geological papers will interest botanists. The zoological papers are of interest chiefly to taxonomic specialists in the groups concerned.—H. C. COWLES.

The geographic botany of Belgium

MASSART's long years of patient study in every part of Belgium have made possible the publication of a splendid treatise on the flora of the country from the standpoint of phytogeography.[6] His previous monograph on the dune vegetation of Belgium is still fresh in the minds of phytogeographers, and the work here noticed is all the more welcome because of the excellent impression made by the earlier volume. This splendid work is dedicated to the memory of ERRERA, and copies were presented to the members of the botanical congress at Brussels. In the introduction the author sets forth his views concerning the methods and purposes of geographic botany, and shows how greatly the methods of ecological geography differ from those of floristic geography. Interesting remarks are made on the relations of "accommodation" to the composition of plant associations.

The first chapter deals with the geology of Belgium, and the second with climate and soil. As is well known, much of the country is of very recent origin, so recent, in fact, that historical records are available as to many points. Under the caption climate there is considered the bearing of various phenological data. The third chapter presents the chief kinds of plant associations that are represented in Belgium. The great density of population of the country for many centuries has greatly modified the natural vegetation cover, yet MASSART has been able to discover and describe a very large number of associations of representative composition, in fact, nearly all that are to be found in western Europe. The chief open associations are found on rocks and on moving dunes, and natural closed associations are represented by heaths, fixed dunes, pans, and bogs. In this part of the volume there are many text figures which illustrate the modification of plants when exposed to diverse conditions. The forests and meadows, as well as the farms and roadsides, are considered under the head of associations modified by human culture. The final chapter considers in detail the various geobotanic districts of Belgium.

---

[6] MASSART, J., Esquisse de la géographie botanique de la Belgique. Rec. Inst. Bot. Léo Errera, tome supplémentaire VII bis. pp. 332. *figs. 99.* With annex containing 216 simple phototypes, 246 stereoscopic phototypes, 9 maps, and 2 diagrams. Brussels. 1910.

The country is relatively poor in glacial relicts, a few being found in the more elevated limestone areas. There is but one endemic seed plant in the country, *Bromus arduennensis*. This work, like others by the same author, is profusely illustrated by remarkable photographs. It is not too much to say that MASSART is the best of ecological photographers.—H. C. COWLES.

The Lower Cretaceous flora

A volume of the Maryland Geological Survey just issued (1911) contains what is perhaps the most complete systematic account, as yet, of the vascular flora of the Lower Cretaceous. The author, EDWARD W. BERRY, has prepared what is in effect a "manual of botany" for the Lower Cretaceous. To traverse what may be regarded as the rubbish of descriptions from all sorts of "impressions," and to obtain from it something of order, is an attempt that deserves commendation, however much opinion may vary as to the result. We have now before us, in convenient form (pp. 295) and illustrated by 76 plates, this most interesting flora as the paleobotanist, who is at the same time a geologist, looks at it.

In the Maryland deposits of the Lower Cretaceous, BERRY has recognized 145 species in 58 genera, and some appreciation of the vastly greater number of recorded species may be obtained from the long lists of synonyms that appear under many species. The only modern generic names in the list are *Selaginella*, *Equisetum*, *Pinus*, *Populus*, and *Sassafras*, though of course numerous names imply resemblances to modern genera. The pteridophytes include 47 of the species, and 44 of these are thought to belong to the Filicales, the other 3 being one species of *Selaginella* and two species of *Equisetum*. The 3 new genera of Filicales proposed are *Knowltonella* (Matoniaceae?), *Dicksoniopsis*, and *Dryopterites*.

The gymnosperms aggregate 63 species, 33 belonging to Bennettitales and 29 to Coniferales, the remaining one being a *Baiera* (Ginkgoales). Among the Bennettitales, *Ctenopsis* and *Dichotozamites* are proposed as new genera, the latter founded upon forms heretofore referred to *Sequoia*. The angiosperms are represented by 35 species, 3 of which (in 3 genera) are monocotyledons, and among these *Alismaphyllum* is a new genus. The 32 species (14 genera) of dicotyledons include *Nelumbites* as a new genus.

In another part of the volume, BERRY summarizes the Lower Cretaceous floras of the world (53 pp.), listing the recorded species in the various countries.

The volume should be very useful to that increasing number of botanists who are becoming interested in paleobotany, for the scattered and chaotic material of this period has been sifted and brought together in more available form.—J. M. C.

Phylogeny of plants

In 1907 LOTSY began the publication of his lectures on the phylogeny of plants, for the use of students of taxonomy. The first volume[7] contained over

[7] See BOT. GAZ. 43:421. 1907.

800 profusely illustrated pages dealing with thallophytes. The second volume[8] appeared in 1909, and contained over 900 pages dealing with the "Cormophyta Zoidogamia," which include, of course, the "polyciliate" gymnosperms. A third huge volume has now appeared,[9] containing over 1000 pages and representing only the first part on "Cormophyta Siphonogamia." The most impressive fact is the publication, within four years, of nearly 2800 pages, which demanded the traversing of an extensive range of literature for the compilation of facts and illustrations.

The present volume deals with Coniferales, Gnetales, and a part of the Angiosperms. There is no occasion for a detailed review, since the volume is an encyclopedia of our present knowledge in reference to these groups, and of the current speculations in reference to their phylogeny. A casual running through the pages indicates that the author has brought together a remarkably wide range of literature, has included a large number of illustrations from scattered contributions, and has organized his material in such a way as to make it easily accessible. The work as a whole will put the student in touch with the most important morphological contributions of recent years, and in this way will serve as a condensed library.—J. M. C.

MINOR NOTICES

Warming's Handbuch.—A third German edition of WARMING'S *Handbuch*, revised by MÖBIUS, has just appeared.[10] This text is so familiar that only the new features of the present revision need be noted. The changes concern chiefly the thallophytes, which MÖBIUS says "have diverged farthest from the original Danish conception," and especially the algae, in the presentation of which the new system of WILLE has been adopted. There are minor changes in other parts, such changes as may take advantage of a revision rather than demand it.

Perhaps the most interesting feature of the volume is the table representing the evolution of the plant kingdom, the blocks indicating the great groups, having the appropriate pigment colors. All the groups are definitely related, the plant kingdom arising from the flagellates, which give rise directly and independently to seven groups ("Chytridiaceae, Myxomycetes, Schizomycetes, Volvocaceae, Conjugatae, Diatomaceae, Peridineae"), the first four groups mentioned being responsible for all the rest. Anthocerotaceae are

---

[8] See *ibid.* 49:225. 1910.

[9] LOTSY, J. P., Vorträge über botanische Stammesgeschichte, gehalten an der Reichsuniversität zu Leiden. Ein Lehrbuch der Pflanzensystematik. Dritter Band: Cormophyta Siphonogamia. Erster Teil. Imp. 8vo. pp. 1055. *figs. 661.* Jena: Gustav Fischer. 1911. *M* 30.

[10] WARMING, EUG., Handbuch der systematichen Botanik. Deutsche Ausgabe. Dritte Auflage, von Dr. MARTIN MÖBIUS. 8vo. pp. xii+506. *figs. 616.* Berlin: Gebrüder Borntraeger. 1911.

responsible for the vascular plants, giving rise directly and independently to three groups ("Filicineae, Lycopodineae, Equisetineae"), the first of which gives rise to the cycadophytes, while the lycopods produce the conifers and these in turn are responsible for the gnetums and the angiosperms. To the modern student of phylogeny this scheme is more interesting than appealing.—J. M. C.

Arm-chair science.—Sir RAY LANKESTER has brought together in book form a group of papers which he contributed to a London daily paper,[11] and which were addressed, of course, to the general public. It is a good illustration of the attitude of the man of science in England, as contrasted with the attitude of his colleagues in the United States. He wishes the public to know of the achievements of science, and this same spirit makes of the British Association a body of great popular interest. Of course "science from an easy chair" is not exact science, for it talks about subjects in an entertaining and suggestive way rather than about demonstrated facts. But still it is a fair question whether the arousing of interest in this way is not justified by the results.

It is of interest to note a zoologist's selection of botanical topics for such presentation. It is as follows: "A rival of the fabled upas tree" (which turns out to be *Rhus Toxicodendron*), "Poisons and stings of plants and animals," "The simplest living things," "The origin of opium," besides general biological topics that pertain to both animals and plants.—J. M. C.

NOTES FOR STUDENTS

Anatomy of Osmundaceae.—GWYNNE-VAUGHAN[12] has found the course of development of the stele in *Osmunda regalis*, *O. palustris*, and a species of *Todea* to correspond very closely to that already described for *Osmunda cinnamomea*. While the details in different individuals are variable, in general it may be said of all that the juvenile stage is long drawn out, and that at least the first pith formed is "stelar," that is, of intrastelar origin. The nodal pockets or parenchymatous pits in the medullary rays, characteristic of the Osmundaceae, are regarded as rather primitive organs and as having arisen independently of the pith. Perhaps the most interesting observation is the fact that some of the earlier leaf traces in *O. regalis* are mesarch. The main part of the paper is devoted to a discussion of the nature of the pith in the Osmundaceae. The author rightly hesitates to draw any far-reaching phylogenetic deductions from the phenomena observed in the sporeling, but prefers to rest his case, in favor of the view that the osmundaceous pith is stelar, on the fossils described by KIDSTON and GWYNNE-VAUGHAN. These fossils include protostelic ferns, in some of which the central tracheids are shorter than the outer ones, and

[11] LANKESTER, SIR RAY, Science from an easy chair. 8vo. pp. xiii+423. *pls.* 2. *figs.* 82. New York: Macmillan. 1911. $1.75.

[12] GWYNNE-VAUGHAN, D. T., Some remarks on the anatomy of the Osmundaceae. Ann. Botany **25**:525–536. *pl.* 44. *figs.* 5. 1911.

siphonostelic ferns in which the medullary rays are narrow or lacking. These feature forms are interpreted as an evolutionary series in which the outstanding is the development of a stelar pith by means of a reduction of the central tracheids and their replacement finally by parenchyma. It would be difficult to prove or disprove this view. That a stelar pith might originate in this way or by an expansion of the stele, as in the roots of many of the higher plants, is unquestioned. But that these fossils represented evolutionary stages which culminated in the conversion of a part of a stelar pith into phloem and endodermis, as in *Osmundites skidegatensis* or *Osmunda cinnamomea*, is unsupported by evidence of any kind.

GWYNNE-VAUGHAN and BOWER accept JEFFREY's hypothesis as to the extrastelar character of the pith in every other family of ferns, but in dealing with the Osmundaceae they cloud the issue by apparently confusing two problems. From a limited series of imperfect fossils they have tried to discover when and how cortical tissues might have been enclosed by the stele. Failing in this, they conclude that they probably could not have been included at all. But neither are we sure when and how that happened in the other families, and a search through the known fossil representatives would probably end as unsatisfactorily as in the case of the Osmundaceae. Research so far has been successful mainly in verifying the theory that the filicinean pith is extrastelar, and with such forms as *Onoclea*, in which the pith consists partly of epidermal tissues and the atmosphere, there is scarcely any escape from accepting it, just as these botanists have done. It is true that the evidence in *Osmunda* is not as striking as in *Onoclea*, but it is quite as striking as in many other forms with extrastelar piths. There are representatives of the Osmundaceae in which the central pith, peripheral pith, internal endodermis, and internal phloem are texturally like those of the outer cortex, inner cortex, external endodermis, and external phloem, and these respectively are continuous at times through leaf or branch gaps. Moreover, there are abundant instances of what in other groups would readily be conceded vestiges of portions of amphiphloic siphonosteles. Applying the same standards of interpretation of anatomical phenomena to all the Filicales, it seems reasonable to maintain that the kind of evidence that has carried conviction in every case but one must hold in all. The question as to when and how the extrastelar pith originated is quite another matter, and I venture to affirm that observations on such features as the relative position of a tracheid and a parenchyma cell in the xylem of a sporeling, or the shape of medullary rays in an adult, will help little in its solution.—J. H. FAULL.

Biology of lichens.—In his culture studies TOBLER[13] used *Cladonia glauca* Floerke and *C. squamosa* (Scop.) Hoffm. By carefully scraping the branches, clusters of soredia were separated. These were sown on sterile

[13] TOBLER, F., Zur Biologie von Flechten und Flechtenpilzen. II. Die Entwicklung der Cladonia-Soredien. Jahrb. Wiss. Bot. 49:409–417. *pl. 3. figs. 11.* 1911.

'earth in flower pots so thickly as to be visible to the eye. The soil was kept from drying by applying distilled water. Cultures of *C. glauca* showed a green growth over the surface of the soil in six or eight weeks. This growth was examined after four months and proved to be a practically pure culture. There was no evidence at this time of development of thallus layers, the structure being gelatinous-granular. The central more moist portion of the culture was green, portions nearer the margin of the pot yellow-white, and the margin white. Microscopic examination showed that the white margin was composed of the lichen hyphae, while other portions of the culture showed the algae present. The thallus layers began to form in six to nine months, the young thalli arising from granules, each of which often arise from two or more soredia. The lichen hyphae were found to become coherent over small areas, and the algae in turn became more deeply seated in the mass. These young squamules were at first few and widely scattered, but later they were seen in large numbers over the surface of the soil.

TOBLER also made a series of cultures on earthen plates. By keeping the air and soil moist in the plate, the hyphae grew luxuriantly. Then he allowed the cultures to dry out for two months. On moistening again, soredia-like masses appeared at certain points over the surface of the soil. Some of these masses were white and composed wholly of lichen hyphae, while others were pale or darker green. These masses increased in size slowly, but did not differentiate into thallus layers.

Hanging-drop cultures were also tried. In three months the soredial masses had grown considerably, and the lichen hyphae were seen radiating beyond the algae in all directions, though the algae had for a time developed more rapidly than the hyphae. Some of the soredia disintegrated and gave rise to many free spherical algae, which he thinks may have passed through a motile condition. Lichen hyphae were seen growing over these algae, but only occasionally attached to them.

The responses to conditions of moisture and light were studied. It was found that soredia from both species would grow luxuriantly after the branches bearing them had been kept in a dry room at about 10° C. for five months. Both the lichen and the algae retained their vitality and grew when moisture was again applied, but the former better than the latter. After cultures had remained in the dark for two or three months, no remains of the algae could be found, while the lichen hyphae had grown well, probably becoming saprophytic on the algae.

TOBLER's results correspond well with what has been observed in nature, where soredia-like growths are often observed growing about patches of *Cladonia*. Like his cultures, these show in some places a pure white color due to strong development of lichen hyphae, and in other places a light or darker green color, depending upon the number of algae present. The soredia grow slowly both in nature and in cultures. A considerable amount of moisture is necessary for the development of the soredium as a whole, yet the soredium

hybrids among the species of the genus. From this statement it is evident that normal fertilization in certain species of *Taraxacum* might be expected.

IKENO[16] has been investigating this situation, and has published recently some of his results. Two species of *Taraxacum* grow in Tokyo, *T. platycarpum* Dahlst. and *T. albidum* Dahlst. During 1908 and 1909, TANAKA, after RAUNKIÄR's method, made castration experiments with the two species and found that *T. albidum* only formed seeds parthenogenetically. In the spring of 1910, IKENO found growing in a field three different varieties of *T. platycarpum* which might perhaps be elementary species in the DEVRIES' sense. With these forms, he performed the following experiments. When the heads were enveloped with sacs, no seeds were matured; which means that in this case there occurred neither self-fertilization, parthenogenesis, nor effective pollination among the flowers in the same head. A similar experiment was tried with *T. albidum*, and the heads with and without sacs produced seeds. Then he took another variety of *Taraxacum* and put sacs around the heads, which later withered entirely. Then he brushed the surface of the heads of the variety before applying sacs, in order to carry the pollen of one flower to another of the same head, and only 5 out of 80 flowers in a head matured perfect seeds; but when the pollen of another head was applied, the majority of the flowers matured seeds. From these experiments he concludes that in *T. platycarpum* there occur no cases of parthenogenesis, while in the other forms of *Taraxacum* cases of parthenogenesis and normal fertilization both occur.—S. YAMANOUCHI.

Inflorescence and ovules of Gnetum.—Mrs. THODAY (SYKES)[17] has investigated the ovulate strobilus and ovules of *Gnetum africanum*, from material obtained by PEARSON during the Percy Sladen Memorial Expedition in southwest Africa. The vascular situation presents some facts of unusual interest. In the nodes of the ovulate strobilus three concentric rings of bundles occur, the middle one being oriented inversely in relation to the other two, and concentric bundles occurring frequently in the two outer rings. The vascular connections of a single ovulate "flower" in *G. africanum* are said to bear "a remarkably close resemblance to the method of supply to the axillary inflorescence in *Bennettites*." A ring of bundles enters the base of the ovule, and finally breaks into three sets, which traverse the three "coverings" of the ovule, the innermost set traversing the inner integument to and sometimes beyond its separation from the nucellus. A well developed pollen chamber is present in the young ovule, and later the apex of the nucellus hardens and forms a pointed cap.

[16] IKENO, S., Sind alle Arten der Gattung *Taraxacum* parthenogenetisch? Ber. Deutsch. Bot. Gesells. **28**:394–397. 1911.

[17] THODAY (SYKES), MARY G., The female inflorescence and ovules of *Gnetum africanum*, with notes on *Gnetum scandens*. Ann. Botany **25**:1101–1135. *pls. 86, 87. figs. 16.* 1911.

The conclusions are that "the radial structure of the seed, the short free apical portion of the nucellus, the presence of a pollen chamber, the extension of the bundle system into the free portion of the inner integument, the complex structure of the outer integument, are all points of contrast with *Welwitschia*, and probably indicate the more primitive nature of the *Gnetum* ovule." Resemblances to *Bennettites* are also pointed out, and the general impression is left that *Gnetum*, *Welwitschia*, *Bennettites*, and *Lagenostoma*, on the basis of ovule structure, are all from some common ancestral stock.—J. M. C.

Annual ring and medullary rays of Quercus.—GROOM[18] has investigated the evolution of the annual ring and medullary rays of the oak, using numerous and widely distributed species, and has reached the following conclusions. The very distinct annual rings of the deciduous species become less marked in evergreen species, but may be recognized by certain structural features that are enumerated, any one or more of which may be lacking. There is an interesting correspondence between the habit and the arrangement of the large vessels in the annual ring. "Species showing the most striking pore-zone are deciduous; those showing it regularly and distinctly, but not having so marked a disproportion in size between the innermost and outermost vessels, are subevergreen; whilst those species with no trace of a pore-zone are truly evergreen." In addition to these categories, there are transitional forms with corresponding transitions in the pore-zone display.

All species were found to possess uniseriate shallow medullary rays, and some possess also broad, high multiseriate rays; and there are numerous transitional stages between these two kinds of rays. The author was not able to decide which type was primitive, the evidence being contradictory as yet. There are cases, as in seedlings of *Quercus* and *Alnus* (BAILEY and EAMES), in which narrow rays form broad ones; other cases, as in *Fagus* (JOST), in which broad rays divide into smaller ones; and still other cases, as in seedlings of *Fagus* (TABOR), in which both kinds of changes go on simultaneously in the rays of the same annual ring.—J. M. C.

Animal parasites of Nepenthes.—An interesting case of symbiosis, somewhat analogous to the presence of intestinal parasites in animals, has been reported by JENSEN.[19] The pitchers of *Nepenthes* have long been known to be partially filled with a fluid containing enzymes in which dead insects seem to be digested, but only with the observations of the present author has attention been directed to the fact that several species of dipterous larvae appear to develop normally in this fluid. So abundant are they that JENSEN declares that of the hundreds of pitchers he has examined from year to year at Tjibodas,

[18] GROOM, PERCY, The evolution of the annual ring and medullary rays of *Quercus*. Ann. Botany **25**:983–1003. *pls. 74–76.* 1911.

[19] JENSEN, HJALMAR, *Nepenthes*-Tiere. II. Biologische Notizen. Ann. Jard. Bot. Buitenzorg Suppl. 3. pt. 2. 941–946. 1910.

he has failed to find a single one without living tenants. These larvae have been reared and studied by MEIJERE,[20] who describes 7 species, of which 6 are new. They are to be referred to the order Diptera, and belong to three different families.

Not the least remarkable characteristic of these larvae is the power they seem to possess of anti-fermentation, and which appears to retard the action of the enzymes of the fluid filling the pitchers. Experiments upon their influence upon the action of solutions of pepsin and pancreatin furnish evidence of their retarding influence. Closely related larvae, taken from pools in the vicinity, were unable to live in the pitchers; hence the anti-ferment is regarded as an adaptation to such symbiotic existence.—GEO D. FULLER.

Grape mildew.—A number of infection experiments, bringing out some of the relations between the downy mildew of the grape and its host, have been described by MÜLLER-THURGAU.[21] Pot-grown grapevines were brought into a greenhouse, and only the new shoots that developed under glass were used for the experiments. The infected shoots were covered for a time with glass cases, to prevent too rapid evaporation of the drops of water containing the spores used for inoculation. The main results of the experiments are the following: No infection took place on the upper surface of the leaves unless punctures had been made in the epidermis. Infections took place readily on the lower surface if the plants were kept in a moist atmosphere. The very youngest leaves were not readily infected, a fact which the author attributes to causes within the leaf rather than to such outer factors as the dense hairy covering. Leaves a little older are most easily infected and in these the fungus grows a long time and forms spots of considerable size before the infected area dies. On the older leaves the action of the fungus is more severe. The infected spots remain small, usually 3–5 mm. in diameter, but the tissue within these spots is killed immediately. In these small spots large numbers of oospores are found. The difference in behavior of leaves of different ages is attributed to differences in moisture content or to differences in composition. —H. HASSELBRING.

Egg-formation in Cystosira and Sargassum.—NIENBURG[22] reports the result of his investigation on the development of the eggs of *Cystosira* and *Sargassum*. *Cystosira barbata* Ag. was collected at Naples in the spring of 1907, and *Sargassum linifolium* was obtained from Triest in September of the following year. The paper presents briefly the nuclear divisions in the oogonium of *Cystosira* and the development of sporelings of *Sargassum*. The author

[20] MEIJERE, J. C. H. DE, *Nepenthes*-Tiere. I. Systematik. Ann. Jard. Bot. Buitenzorg Suppl. 3. pt. 2. 917–940. 1910.

[21] MÜLLER-THURGAU, H., Infection der Weinrebe durch *Plasmopara viticola*. Centralbl. Bakt. II. **29**:683–695. *fig. 1.* 1911.

[22] NIENBURG, WILHELM, Die Oogonentwicklung bei *Cystosira* and *Sargassum*. Flora **1**:167–180. *pls. 1, 2. figs. 9.* 1910.

followed the nucleus in the oogonium of *Cystosira* from the young resting stage to synapsis, metaphase of the first division, and second and third divisions. The number of chromosomes in the first division he reports to be 18–20. He compares the figures of the first division with those of vegetative divisions, and because of the appearance of a much higher number of chromosomes in the vegetative figures, he infers that 18–20 is the reduced number. Further, upon comparison with the case of *Fucus*, he infers that the oogonium of *Cystosira* and *Sargassum* may represent the x-generation. The development of the sporelings of *Sargassum* is discussed in comparison with SIMONS' work on another species of the same genus. The reviewer thinks that it is very desirable to have more detailed accounts of the events occurring in the oogonium of these forms and of the processes connected with the development of a normally fertilized or a parthenogenetic egg.—S. YAMANOUCHI.

Spermatogenesis in liverworts.—WOODBURN,[23] while studying spermatogenesis in *Porella*, traversed the work of IKENO, ESCOYEZ, and SCHAFFNER in *Marchantia polymorpha* and that of BOLLETER in *Fegatella conica* for evidences of centrosomes. In none of the forms studied did he find any evidence of centrosomes. Although occasional granules were found in the cytoplasm, or in the region of the spindle, they did not present the appearance of or behave like centrosomes. He concludes that if a body does sometimes occupy the pole of a spindle it does not imply that it is any more a centrosome than the other bodies scattered through the cytoplasm. He says that the blepharoplast develops *de novo* from a dense granular or spherical mass, kinoplasmic in origin, located usually at the most distant angle of the spermatid. The blepharoplast becomes a cord, growing in close contact with the plasma membrane. He thinks the "cytoplasmatischer Fortsatz" of IKENO is merely a part of the blepharoplast. Nothing whatever corresponding to a "Nebenkörper" was found. He concludes that the sperm at maturity represents the two constant cell elements, nucleus and cytoplasm; that the main body of the cell represents the nucleus; that the blepharoplast and cilia represent specialized cytoplasm; and that the remainder of the cytoplasm is found in the vesicle.—W. J. G. LAND.

Records of Oenothera.—GATES[24] has undertaken to trace the history of species of *Oenothera* in cultivation, particularly the large-flowered forms. This involved a critical examination of the records through three centuries, beginning with TOURNEFORT'S *Institutiones*. The pertinent evidence is recited from the documents in detail, and the conclusion reached that "a form closely resembling *O. Lamarckiana* was the first *Oenothera* introduced into Europe

[23] WOODBURN, W. L., Spermatogenesis in certain Hepaticae. Ann. Botany **25**: 299–313. *pl. 1.* 1911.

[24] GATES, R. R., Early historico-botanical records of the Oenotheras. Proc. Iowa Acad. Sci. **17**:85–124. *pls. 6.* 1910.

from Virginia (about 1614), and therefore that it did not originate in cultivation." Since the writing of the paper, the author has had an opportunity to examine type specimens and early collections in London, and is now inclined to believe that this "first *Oenothera*" was rather the European *O. biennis*, with somewhat large flowers but shorter style. It is of further interest to note in the paper that the author regards *O. Lamarckiana* and all open-pollinated forms as hybrids and not pure races, in the sense that they have undergone crossing in nature as well as in gardens. This means that the important matter to investigate is the relation between this crossing and the phenomena of mutation. At the same time, the author does not believe that there is evidence for regarding *O. Lamarckiana* as an ordinary synthesized hybrid, produced by the crossing of such forms as *O. grandiflora* and *O. biennis*.—J. M. C.

Influence of aspect on vegetation.—From a careful study of the distribution of various plant associations and plant species on the mountain sides of southern Arizona, BLUMER[25] states as a general truth that reversion of aspect takes place with change of altitude. Various species of oak and pine furnish much of the evidence upon which this generalization is based, hence the distribution of *Quercus reticulata* upon the Santa Rita Mountains may be cited as an example. It is first found in shaded situations upon north slopes at 6000 feet, and becomes common as a tall clean coppice form at 6500 feet, spreading to the east and west slopes. At 8000 feet it is practically absent from the north side, is abundant on the east and west, and has begun to appear freely on the south side, where it continues as a chaparral growth to an altitude of 9400 feet. A similar change of aspect is exemplified in the occurrence of various other species. The factor concerned in these changes of aspect is the difference in isolation.

The species studied seem to have occupied all the space they are capable of doing, those with the widest range of variations in form and structure having, by virtue of their plasticity, the widest distribution, but even to such forms no extension of range seems possible while the present topography and climate endure.—GEO. D. FULLER.

Orchid bulbs as fungicides.—Small portions cut from the bulbous parts of certain orchids appear to have a toxic effect upon the mycorhiza of the same plants. In experimental cultures conducted by BERNARD[26] they were very fatal to the hyphae of some species of the fungi, destroying all that came in contact with the fluids diffusing from the bulbous material. Certain other species of fungi isolated from orchid roots proved more resistant, fatal effects being evident only in the presence of larger masses cut from the bulbs. Heated

[25] BLUMER, J. C., Change of aspect with altitude. Plant World 14:236–248. 1911.

[26] BERNARD, NOEL, Sur la function fungicide des bulbes d'Ophrydées. Ann. Sci. Nat. Bot. IX. 14:221–234. 1911.

to 55° C. the toxic properties seem to have been destroyed, which together with other data leads to the conclusion that the substance acting as a fungicide is an enzyme. It serves to explain the fact that no endophytic fungi are found in the bulbous portions of various orchids, although they are always present in the roots of the same plants, thus conforming to BERNARD's hypothesis that these orchids are plants which tolerate the mycorhiza, while at the same time they are able to defend themselves against their complete invasion. These investigations were still in progress when they were interrupted by the death of the brilliant scientist who has contributed so largely to the understanding of the symbiosis existing between various endophytic fungi and their hosts.—GEO. D. FULLER.

Vegetation of islands and peninsulas.—From a brief study of the irregular shore line of Lake Tsala Apopka, Florida, and an examination of the literature on the vegetation of the Atlantic coastal plain, HARPER[27] finds that the peninsulas and islands are almost universally characterized by a vegetation of a climax type composed largely of broad-leaved evergreen trees, among which *Magnolia grandiflora* and *Quercus* spp. are conspicuous. This is in striking contrast with the pine forests which occupy the adjacent mainland. Several possible hypotheses in explanation of this phenomenon are examined and rejected, as fire seems to the investigator to afford an adequate key to the situation. Fires would doubtless be of much less frequent occurrence upon islands and peninsulas than upon the more continuous mainland, and this circumstance would permit a more rapid advance toward mesophytism, but it seems possible that differences of soil moisture and evaporation due to the proximity of considerable bodies of water and to the slight elevation of the islands and peninsulas above their surface may have been at least secondary factors in hastening the development of the climax vegetation.—GEO. D. FULLER.

Phylogeny of algae.—BRUNTHALER[28] has discussed the phylogeny of algae, based upon results he obtained from culture experiments and those obtained by ENGELMANN, OLTMANNS, STAHL, PÜTTER, and others. A brief summary of his conclusions is as follows: (1) The chromophyll and chlorophyll of Rhodophyceae, Phaeophyceae, Zygophytae (including Peridinales, Bacillariales, and Conjugales), are the result of adaptation to light intensity since these forms first appeared. (2) The modern Flagellatae are end structures from the oldest organisms, but the direct relationship of the modern flagellates with these ancient organisms cannot be demonstrated. (3) The Rhodophyceae are to be regarded as phylogenetically the oldest group of algae, and their ancestors have come from the primitive forms of flagellates. (4) The Phaeo-

[27] HARPER, ROLAND M., The relation of climax vegetation to islands and peninsulas. Bull. Torr. Bot. Club 38:515–525. 1911.

[28] BRUNTHALER, JOSEF, Zur Phylogenie der Algae. Biol. Centralbl. 31:225–236. 1911.

phyceae are the next younger group of algae, descended partly from Rhodophyceae and partly from flagellate-like organisms. (5) The Zygophyceae are derived from flagellated ancestors, the Peridinales being most nearly related to the modern flagellates. (6) The Chlorophyceae are the youngest of the algae, and have come partly from Rhodophyceae and partly from flagellated ancestors.—S. YAMANOUCHI.

Sporangia and spores of Aneimia.—STEVENS[29] has investigated the development of the sporangia and spores in a species of *Aneimia*. He finds that the two tapetal layers break down at the mother cell stage, freeing the protoplasts and resulting in a tapetal plasmodium, as among the Ophioglossales. It was in connection with work on *Botrychium* (1906) that STEVENS proposed the excellent descriptive phrase "tapetal plasmodium." Perhaps it was a slip that he did not include this earlier paper in the "literature cited," or the still earlier paper of CARDIFF (1905). Upon the separation of the mother cells in *Aneimia* the plasmodium entirely surrounds each one. As each mother cell lies imbedded separately in the plasmodium, no wall is seen, and when the tetrad is formed the mother cell membrane persists about it. At the separation of the spores of a tetrad, the tapetal plasmodium flows between them. The author thinks that the thickness of the exine "is the work of the tapetal plasmodium." It is becoming more and more evident that in structure and behavior the Ophioglossales and Filicales belong together.—J. M. C.

Chromosomes in maize.—KUWADA[30] has studied the nuclear conditions in the pollen mother cells of nine different races of corn: red starch corn, yellow starch corn, amber rice popcorn, black starch corn, golden broach field corn, white flint corn, sugar corn, early light sugar corn, and red sugar corn. The number of gemini in these different races varies from 9 to 12, the sugar corns having generally a larger number than the starch corns. He thinks that the smaller number was reduced from 12, which is the original number for all the races of *Zea Mays*. The size and shape of the gemini in a figure differ, and there is present always a duplication of each of the gemini. In the equatorial plate of the homotypic division some pairs of chromosomes come in contact with each other. He suggests that the production of innumerable races of *Zea Mays* might have a certain relation to the duplication of chromosomes, resulting in the double number derived from the original form, which had probably 6 chromosomes as the reduced number.—S. YAMANOUCHI.

Botryopteris antiqua.—This interesting paleozoic fern, described by KIDSTON in 1908 from inadequate material, has been studied by Miss BENSON[31]

[29] STEVENS, WILLIAM CHASE, On the development of the sporangia and spores of *Aneimia phyllitidis*. Ann. Botany **25**:1059–1068. *pls. 84, 85.* 1911.

[30] KUWADA, Y., Maiosis in the pollen mother cells of *Zea Mays* L. Bot. Mag. Tokyo **25**:164–181. *pl. 6. figs. 4.* 1911.

[31] BENSON, MARGARET, New observations on *Botryopteris antiqua* Kidston. Ann. Botany **25**:1045–1057. *figs. 3. pls. 81–83.* 1911.

from a more abundant collection. The axis was rhizomatous, giving off numerous roots at intervals, and bearing two kinds of leaves, one set of petioles being supplied by a monarch leaf trace, and the other set by a diarch trace. The smaller leaves, supplied by the monarch trace, show at base a sheathing organ which is thought to represent the so-called aphlebia of *Zygopteris;* if so, this is the first record of the structure in *Botryopteris*, and further emphasizes the relationship of the two genera. BERTRAND'S view that the simple stele of *B. antiqua* is due to reduction and not to its primitive character is objected to. As the author says, "this view involves the assumption that the diarch type of petiole is older than the monarch, and the species (*B. antiqua*) is in process of simplification. This result is not easy to harmonize with the fact that later forms of *Botryopteris* petiole are triarch."—J. M. C.

Origin of transfusion tissue.—The so-called transfusion tissue of the leaves of gymnosperms has been recognized for many years as an anatomical feature of the group. WORSDELL (1897) suggested, on the basis of distribution and nature, that it is a modified centripetal xylem. Since the presence of centripetal xylem is an important fact in discussing evolutionary sequences, this view extended the range of recognizable centripetal xylem. Now Miss CARTER[32] has studied the beginnings of this tissue in the cotyledons, using 13 species, representing 9 genera of conifers. The conclusion is "that the first-formed transfusion tracheids appeared in such positions and were of such size as to make it appear improbable that they arose, in these organs at any rate, as an extension of the development of the centripetal wood." The evidence from a comparison with the other elements of the vascular strand suggests that "transfusion tissue" develops from the parenchyma.—J. M. C.

The causes of thorn development.—Since LOTHELIER conducted his researches on the experimental morphology of thorns, it has been generally believed that their development is favored and even caused by abundant light or by atmospheric desiccation. This was supposed to be the case particularly in the gorse, *Ulex europaeus*. ZEIDLER now calls these results in question,[33] for he is able to secure the development of thorns in *Ulex* both in partial darkness and in moist atmosphere. He regards the leafy shoots secured by LOTHELIER in moist air and in darkness merely as juvenile forms, whereas the thorny shoots are regarded as adult forms. It may be remarked that, even if further experiment should confirm the views of ZEIDLER, the real problem is in no wise touched by his experiments. It would still remain to determine why "juvenile shoots" should appear at some times and "adult shoots" at other times.—H. C. COWLES.

---

[32] CARTER, M. GERALDINE, A reconsideration of the origin of "transfusion tissue." Ann. Botany 25:975–982. *figs. 4.* 1911.

[33] ZEIDLER, J., Ueber den Einfluss der Luftfeuchtigkeit und des Lichtes auf die Ausbildung der Dornen von *Ulex europaeus* L. Flora 102:87–95. 1911.

Swamp vegetation in Japan.—A study of the vegetation of a shallow lake by NAKANO[34] is probably the first ecological investigation to be reported from Japan. The lake represents an ox-bow of the River Tone, and is surrounded by a swamp formation consisting of four concentric zones about the central association of submerged plants, among which various species of *Potamogeton* predominate. The succeeding associations are characterized by *Zizania aquatica*, *Typha angustifolia*, *Phragmites communis*, and *Sagittaria sagittifolia* respectively. The author decides from an analysis of the swamp flora that its closest alliance is with that of China, with 67 per cent of common species; the dominant species, however, are mostly common to North America, although the analysis shows only 27 per cent of common species. The only endemic plant is *Potamogeton lucens* var. *teganumensis*.—GEO. D. FULLER.

Mycorhiza of Solanums.—Seeking for data which could be related to his hypothesis of tuberization being caused by fungal infection, BERNARD[35] had begun the investigation of the various species of *Solanum* for the presence of endophytic fungi when death interrupted his labors. He found, however, that such fungi were present in the rootlets of older plants of *Solanum Dulcamara*, and in the roots of the probable ancestor of the cultivated potato, *S. Maglia*. The latter showed the presence of mycorhiza only when growing under natural conditions, being entirely free from infection as cultivated in botanic gardens and elsewhere in Europe. These results are suggestive of the possible effects of cultivation upon the fungi present in the tubers of the potato, and of their possible influence upon the evolution of tuberization as it now exists in the potato.—GEO. D. FULLER.

Vascular connections of sporocarp of Marsilea.—Ever since the "fertile spike" of Ophioglossaceae has been removed by CHRYSLER and others from the category of an adaxial sporangiophore to that of fused lateral pinnae, the adaxially stalked sporocarp of the Marsileaceae has been a suggestive situation. CHRYSLER studied *Marsilea quadrifolia* and found the vascular connections of the sporocarp stalk to be the same in kind as those of the fertile spike in Ophioglossaceae. Miss ALLISON[36] has now added *M. polycarpa*, in which the petiole bears a varying number of sporocarps, which arise acropetally. She finds that the vascular connections are just as in *M. quadrifolia*, and indicate that the sporocarps are fertile lobes of the leaf. She found also the same condition in *Pteris semipinnata*, a species with pinnules on one side only of the pinna.—J. M. C.

---

[34] NAKANO, H., The vegetation of the lakes and swamps in Japan. I. Teganuma. Bot. Mag. Tokyo 25:35–51. *figs. 6.* 1911.

[35] BERNARD, NOEL, Les mycorhiza des *Solanums*. Ann. Sci. Nat. Bot. IX. 14: 235–257. 1911.

[36] ALLISON, HARRIET E., Note on the vascular connections of the sporocarp in *Marsilea polycarpa* Hook. and Grev. New Phytol. 10:204–206. *pl. 3.* 1911.

and states that the nuclei of the male and female plants were in all cases apparently identical, both in the number and in the character of their chromosomes. More complete studies have been made by DARLING (5) in *Acer Negundo*, and by STRASBURGER (38) in *Melandrium rubrum*, *Cannabis sativa*, *Mercurialis dioica*, and *Bryonia dioica*. Both writers report that in the reduction division of the microspore mother cells they find no evidence of anything which might be considered a "sex determinant." Negative results in these few cases, of course, do not prove that a sex determinant never occurs in plants, for it will be remembered that such a condition has been demonstrated in only a comparatively few animals.

Dimorphic heterostylous plants present, as will be pointed out below, such striking resemblances to dioecious plants that the present study was undertaken in the hope of finding, in the reduction division of the microspore mother cells, some indication of a morphological difference in the chromosomes which go to make up the nuclei of the microspores.

Material of several species was prepared, but only two, *Fagopyrum esculentum* and *Houstonia caerulea*, proved favorable for study. The material used was all collected in the spring and summer of 1910. The buds of *Fagopyrum* were taken from vigorous plants under cultivation; those of *Houstonia* were nearly all from an old, well-established lawn, where many of the clumps had very likely persisted for several years.

The writer wishes to acknowledge his indebtedness to Professor A. W. EVANS, at whose suggestion this study was undertaken, for assistance in all parts of the work, and to Dr. G. E. NICHOLS for generous aid in the collection and preparation of material.

Historical sketch

PERSOON, in 1794, notes that in certain species of *Primula* there are two forms which exist in about equal numbers and differ from each other in the length of their pistils and stamens. This is, according to VON MOHL (p. 326), the first description of the condition now known as heterostyly.

This condition was apparently regarded as a mere variation in form until the time of DARWIN, who discusses several dimorphic

and trimorphic genera in a series of papers read before the Linnean Society during the years 1862–1868. In these early papers DARWIN (**6–10**) calls attention to the fact that the morphological differences in the flowers constitute a device by which cross pollination is favored, and that these differences in form are associated with physiological differences which affect their fertility, so that a flower of either form is more likely to be fully fertilized when pollinated from a flower of the other form ("legitimate pollination") than when pollinated from a flower of the same form ("illegitimate pollination"). He also describes the offspring of illegitimate unions and points out that they differ from normal plants and have what he calls a "hybrid-like" nature.

DARWIN afterward collected these papers and published them in a "connected and corrected form, together with new matter" in *The different forms of flowers in plants of the same species*, which contains also an account of the literature on the subject up to the date of its publication (1877). Only three of the writers whom he mentions, HILDEBRAND, SCOTT, and MÜLLER, treat heterostyly as anything more than a mere difference in form or at most a device to favor cross pollination.

HILDEBRAND, who first used the term "heterostyled," was also the first to investigate the inheritance of heterostyly. In his first paper (**18**) he describes experiments on the illegitimate fertilization of *Linum perenne* and *Primula sinensis*. The illegitimately pollinated flowers of *Linum* were uniformly sterile. In *Primula*, however, all the illegitimately pollinated flowers developed capsules, which contained an average of 18 seeds, about two-fifths the number found in the capsules of legitimately pollinated flowers. HILDEBRAND planted the seeds thus produced, and found that while the seeds of either form legitimately fertilized produce long-styled and short-styled forms in about equal numbers, the seeds from illegitimate unions tend to reproduce the parent form. Seeds from illegitimate unions of long-styled plants, however, tend to transmit the parent form more truly than those of the short-styled. This conclusion was accepted by DARWIN, but the results he later obtained from similar experiments with *Primula sinensis* do not agree very closely with those of HILDEBRAND.

Two later papers by HILDEBRAND (**19, 20**) deal with trimorphous species of *Oxalis*. He found in *Oxalis Valdiviana* (**20**, p. 43) that seeds from any one of the six possible legitimate unions produced all three forms, but that the two parent forms greatly predominated. He also states that long-styled plants of *Oxalis rosea*, growing by themselves, have always produced long-styled plants ("Jahr aus Jahr ein dieselbe Form entsteht").

In 1864, JOHN SCOTT published a paper (**32**) in which he arranges all the known species of *Primula* in four groups: dimorphic, short-styled, long-styled, and non-dimorphic (homostyled), and describes experiments with 7 dimorphic species. He pollinated each of these 7 species both legitimately and illegitimately and counted the seeds obtained by each method. The result was uniformly that legitimate unions produced a markedly greater number of seeds than illegitimate.

FRITZ MÜLLER (**27**), in a brief paper dealing with a trimorphous species of *Pontederia* growing in Brazil, mentions the fact that in *Oxalis Regnelli*, another trimorphous species, the seeds of long-styled plants, legitimately fertilized with pollen from the longest stamens of the mid-styled form, produced plants which belonged exclusively to the two parent forms.

In his *Forms of flowers*, DARWIN includes all that had been done on heterostylous plants up to the time of its publication. He cites 38 genera known to include heterostyled species. These genera are distributed as follows (**11**, p. 254): Hypericineae 1, Erythroxyleae 2, Geraniaceae 2, Lythraceae 2, Rubiaceae 17, Primulaceae 3, Oleaceae 1, Gentianaceae 3, Polemoniaceae 1, Cordieae 1, Boragineae 1, Verbenaceae 1, Polygoneae 1, Thymeleae 1, and Pontederiaceae 1. The wide geographical distribution of the genera which contain heterostyled species and the fact that the families to which they belong are mostly very distinct from one another, indicate that heterostyly has arisen independently in several phylogenetic lines.

DARWIN considers (p. 245) that the morphological differences between the forms of a heterostyled species are confined to the flower. His observations on this point may be summed up briefly as follows: In the calyx there are no differences. The corolla

shows slight differences in shape due to the different position of the anthers. In *Pulmonaria* there is also a slight difference in the size of the corolla, and in *Pontederia* in its color. The most striking differences, of course, occur in the stamens and pistils (p. 247). The pistils differ in length of style and in size and shape of stigma. The stamens show a corresponding difference in length of filament or in place of insertion; and there is sometimes a difference in the color and thickness of the filaments, and in the size of the anthers. The pollen grains usually show a marked difference in size in the different forms. Of 43 cases cited, only 8 showed pollen grains of equal size in the different forms. In all the others the size of the pollen in the short-styled form exceeded that of the long-styled form (p. 249). The greatest difference was found in a trimorphous species of *Pontederia*, in which the diameters of the pollen grains from the longest stamens are to those of the shortest as 100:55, indicating a difference in contents in the ratio of 6:1.

These morphological differences are slight, however, compared with the physiological differences which accompany them. Repeated experiments have shown that complete fertility in heterostylous plants is secured only when a flower is pollinated with pollen from a flower of another form, that is, the pollen must come from a stamen equal in length to the pistil on which it is placed. The superiority of legitimate over illegitimate pollination is shown by the proportion of flowers which yield capsules and by the average number of seeds per capsule (p. 245). As DARWIN himself states, morphological characters alone do not furnish conclusive evidence of heterostyly. Final proof can be derived only from experiments which show that pollen must be applied from one form to the other in order to insure complete fertility.

The physiological difference in the forms is exhibited also in the time necessary to secure fertilization with legitimate and illegitimate pollen. DARWIN (p. 31) placed on several stigmas of a long-styled cowslip plenty of pollen from the same plant, and after 24 hours added some from a short-styled dark red polyanthus. From the flowers thus treated, 30 seedlings were raised, and all, without exception, bore reddish flowers. DARWIN describes a still more striking difference in *Linum perenne* (p. 87). He placed pollen

from a long-styled flower on all 5 stigmas of a long-styled flower on a separate plant. After 19 hours the stigmas were dissected and only a single pollen grain had emitted a tube. The pollen proved to be good when placed on the stigma of a short-styled plant. This experiment was repeated three times, with uniform results. A similar condition has been shown to occur in *Lythrum Salicaria* by STRASBURGER (**34**, p. 82). In this plant illegitimate pollination resulted in only a very slight growth of the pollen tube.

Physiological differences appear also in ways which less directly affect fertilization. In the long-styled form of *Linum perenne* (DARWIN, **11**, p. 130), each separate stigma rotates on its own axis when the flower is mature, thus turning its papillose surface outward. This movement is confined to the long-styled form. In *Faramea* the stamens of the short-styled form rotate on their axes. No such motion is found in the stamens of the long-styled form.

DARWIN'S experiments on the inheritance of heterostyly, like those of the other earlier workers, do not give very uniform results. But he deduces the general laws that seeds from illegitimate unions tend to reproduce the parent form (p. 271), and that illegitimate unions of long-styled plants tend to transmit the parent form more truly than do those of short-styled plants.

Recently, BATESON and GREGORY (**2**) have experimented on the inheritance of heterostyly in *Primula*. They find that in *Primula sinensis* the inheritance follows the Mendelian type, the short style being the dominant character and the long style the recessive. Short-styled plants are then heterozygotes, and half their gametes bear the dominant character, the other half the recessive; while long-styled plants are homozygotes and all their gametes bear the recessive character. One remarkable exception, however, was found. This was a single short-styled plant in which the female gametes were normal, that is, half bore the dominant and half the recessive character, while the male gametes bore the dominant character almost exclusively. BATESON and GREGORY note, as did DARWIN, that about half the eggs are fertilized by illegitimate pollen, while the rest are not; and suggest that this may be due to a differentiation of the egg cells of the plants.

ERRERA (**13**) has pointed out that *Primula elatior* shows what

he calls "caractères hétérostyliques secondaires." That is, the two forms differ not only in the parts of the flower, but also in the forms of the leaves. As he describes them (p. 229), the leaves of the long-styled form are "relatively longer and narrower, the ratio of the mean length (measured from the base of the petiole to the tip of the blade) to the maximum width being 2.86:1, and in plants grown in deep shade, 3.63:1"; while the leaves of the short-styled form are "relatively wider and shorter, the ratio of the mean length to the maximum width being 2.41:1, and in plants grown in the shade, 3.11:1."

Relation of heterostyly to dioeciousness

Dimorphic heterostylous plants present, in several respects, a striking resemblance to dioecious forms. In other hermaphrodite plants and in hermaphrodite animals, there is presumably unlimited possibility of crossing. In dimorphic heterostyled plants, however, the individuals are divided into two classes, which exist in approximately equal numbers and are adapted for reciprocal fertilization, a condition essentially the same as that found in dioecious plants and in the higher animals. This resemblance is made still more evident by ERRERA'S recent discovery of differences in the vegetative organs of the two forms in *Primula elatior*, comparable to the secondary sexual characters common in animals and found in a few dioecious plants, such as the hemp.

Naturally, no very definite comparison can be drawn between the inheritance of heterostyly and the inheritance of sex until it is decided what laws the inheritance of sex actually follows. But it may at least be pointed out that the condition described by BATESON and GREGORY for *Primula sinensis*, in which one form is a heterozygous dominant and the other a homozygous recessive, is exactly the condition believed, by several workers, to exist in the inheritance of sex, notably by CORRENS (**4**) for the dioecious *Bryonia alba*, and by BATESON for animals (Wilson **40**, p. 63). Aside from any analogy with dioecious plants, the work of BATESON and GREGORY on *Primula sinensis* indicates that in this form, at least, the inheritance follows the Mendelian law, a condition which indicates that a segregation of different characters occurs in the

reduction division of both megaspores and microspores of one form, in this case the short-styled form. Whether this is accompanied by any morphological difference in the chromosomes or not is of course another question.

The resemblance of dimorphic heterostylous plants to dioecious plants suggested to DARWIN (p. 285) that heterostyly may have been one of the ways by which the dioecious condition among flowering plants was attained. He cites several cases of plants which are dioecious, but show indications of a heterostylous ancestry. *Asperula scoparia*, an inhabitant of Tasmania, is dioecious, but the male flowers have large anthers and a very small pistil with rudimentary stigma and style, while the female flowers have a large, well-developed ovary and rudimentary anthers apparently quite destitute of pollen. *Discospermum*, of Ceylon, is apparently heterostyled, but one of the two forms is always barren, the ovary containing about two aborted ovules in each loculus, while in the other form each loculus contains several perfect ovules. The species is therefore really dioecious. Most of the species of the South American genus *Aegiphila* are heterostyled. In *Aegiphila obdurata*, however, the anthers of the long-styled form are entirely destitute of pollen, while the pistil is perfectly developed; in the short-styled form, on the other hand, the pistil is aborted, while the stamens are perfect.

There are a number of facts which indicate (BLAKESLEE **3**, p. 371) that in all dioecious plants one sex is dominant and makes its appearance while the other remains latent. Male and female willow plants are frequently found with flowers of the opposite sex. *Lychnis dioica* is normally dioecious, but STRASBURGER (**35**, p. 692) found in his cultures at Bonn occasional hermaphrodite plants. These were in every case affected by a smut, *Ustilago violacea*, and he attributes the hermaphrodite condition to the action of the fungus. *Ustilago violacea* fruits only in the anthers of the host plant. If it attacks a male plant it fruits in the anthers, and if it attacks a female plant, in some way it stimulates its host to the production of stamens, in which it fruits.

Recently SHULL (**32**, p. 112) has described occasional hermaphrodite plants occurring in a pure bred normal race of *Lychnis*,

in which *Ustilago violacea* has never appeared. He reverses (p. 119) STRASBURGER's interpretation of the origin of the diseased hermaphrodites, and suggests that the infected plants were males in which the disease allowed the pistils to develop. SHULL's discovery that hermaphrodite plants arise occasionally in normal races and his criticism of STRASBURGER's interpretations do not alter the importance of the fact that in a normally dioecious plant the bisexual condition may sometimes occur, perhaps because of some pathological stimulation. Another instance of the same condition is cited by STRASBURGER (**38**, p. 471). He reports, in the normally dioecious *Mercurialis annua*, male plants bearing a few female flowers, some of which when pollinated produced good seed.

The condition just described would seem to indicate that dioecious plants arose from the hermaphrodite condition. If such is the case, dimorphic heterostylous plants, since they already exist in two classes, which differ considerably and are adapted for reciprocal fertilization, might be more likely to become dioecious than would homostylous plants.

In this connection it is tempting to extend LILLIE's view of the origin of sex to the origin of dioeciousness in the higher plants. He assumes (**23**, p. 375) that fertilization may be always selective, even when there is no morphological gametic differentiation. According to his idea, gametes may be physiologically different even when they are morphologically alike. Morphological differentiation would then follow naturally, as the expression of these physiological differences, and sex differentiation as a further stage in the same process of evolution.

Is it not entirely probable that different "strains" may exist in some species of hermaphrodite plants which differ in their relations of fertility somewhat as do the different "forms" of heterostylous plants? Panmixia has always been assumed to be the natural condition of hermaphrodite species. That is, it has been assumed that any individual can fertilize or be fertilized by any other individual in the species with equal ease, but that such is actually the case has never been proven. The existence of different "strains" having such relations as suggested above would not be easily demonstrated under natural conditions, as each stigma

doubtless receives pollen from several flowers, among which it could easily "select" the favorable pollen, by inducing a more rapid growth of the pollen tube of the "legitimate" kind, exactly the method by which illegitimate fertilization is prevented, under normal conditions, in heterostylous plants.

The morphological differences shown by the different forms of heterostylous plants are really very slight compared with their physiological differences. According to the view suggested above, dimorphism, trimorphism, and dioeciousness would be merely morphological expressions of physiological differences common to many plants. Such an hypothesis would account for the origin of dioeciousness and heterostyly at different points, widely separated both geographically and genetically throughout the plant kingdom.

Fagopyrum esculentum

The dimorphous flowers of the buckwheat were first described and very accurately figured by HERMANN MÜLLER (**28**, p. 165; also **29**, p. 509). As MÜLLER points out, there are "in each form 8 stamens, 3 closely surrounding the styles and opening outwards, the 5 others inserted more outwards and opening inwards." The place occupied in one of the forms by the anthers is occupied in the other by the stigmas, a perfect adaptation for cross pollination by the numerous insects which visit the flowers for the sake of the honey secreted by the 8 globular nectaries at the base of the filaments. There is apparently no difference in the structure of the stigmas in the two forms, but the pollen grains of the short-styled form are larger than those of the long-styled form, their diameters being in about the ratio 5:4. There appear to be no secondary differences in the vegetative structure of the plants.

The flowers are as a rule true to form, and there is no difficulty in distinguishing long-styled from short-styled plants. Occasional flowers with the stigmas at the anther level, however, are seen on normal long-styled plants. Seldom more than one such flower occurs on a plant and this is usually the first which opens. A similar condition has been noted by BATESON and GREGORY in *Primula* (**2**, p. 583). One plant, however, was noted among some grown

for experimental purposes in the greenhouse, which showed such unusual floral variations as to be worthy of record. The plant produced 10 blossoms, and 8 of these had stamens and pistil both long; while 2, the third and eighth, were normal short-styled flowers. The earlier blossoms were removed in order to secure continued flowering. Later, however, two of the abnormal flowers were pollinated, one with pollen from a short-styled and the other with pollen from a long-styled flower, but neither developed seed. One of the normal short-styled flowers on this plant, however, produced a good seed when self-pollinated.

It will be noted that in both the cases cited above, in which the stamens and pistil are of the same length, it is the pistil which has varied from its normal length. That is, if a flower on a short-styled plant shows pistils and stamens of equal length, both are long; while in such a flower on a long-styled plant, both pistil and stamens are short. A curious case which shows a similar variation in the length of the pistil has been noted by BATESON and GREGORY (**2**, p. 583) in *Primula sinensis*. There is a variety with a very large yellow "eye" extending up over the limb of the corolla, quite distinct from the small yellow pentagon characteristic of the normal flower. This variety has the anthers in the position normal for long-styled plants, but the style is short and the stigma just reaches the anther level, a condition which BATESON and GREGORY designate as "equal-styled." In investigating the inheritance of these two unusual characters, they find that the "equal-style" is the form which the long-styled type assumes when the plant is homozygous in the large eye character. In this case, as in the others mentioned, the pistil alone varies from the normal length.

DARWIN experimented in a rather imperfect manner on the relative fertility of the two forms in the buckwheat, and showed that illegitimate fertilization is less successful than legitimate, yielding fewer and smaller seeds. In order to gain some knowledge of the relative ease of legitimate and illegitimate fertilization, the following experiment was made. Plants were grown from seed in a greenhouse, where there were no insects which might bring about pollination. The flowers which were to be experimented upon were examined with a lens in order to make pistils

had not been accidentally pollinated, and were castrated to prevent self-pollination. They were then pollinated artificially, either with pollen from a plant of the other form "legitimately," or with pollen from another plant of the same form "illegitimately."

After a definite number of hours, the pistils were fixed and microtone sections prepared. In the case of legitimate pollination, pistils fixed 18 hours after pollination showed regularly a 3-celled pro-embryo, and at least three free nuclear divisions had occurred in the endosperm. The embryo was usually in the quadrant stage 24 hours after legitimate pollination. The time elapsing between pollination and fertilization seems to have no relation to the distance traveled by the pollen tube, for it did not differ perceptibly in the two forms.

Pistils which had been illegitimately pollinated showed when sectioned that in 24 hours the pollen tube had made but a very slight growth. After 48 hours there was a greater development of the pollen tube; and in 3 days (72 hours) a few pistils showed the pollen tube extending nearly to the egg. Some of the pistils which were fixed 96 hours after illegitimate pollination showed the embryo in the 8- or 16-celled stage.

Under the conditions of the experiment then, if pollen from either form was placed on the stigma of a flower of the other form, the growth of the pollen tube and the fusion of the two nuclei required considerably less than 18 hours. But if pollen from either form was placed on the stigma of a flower of the same form, even though on a different plant, a period longer than 3 days was required for the tube to reach the egg. Illegitimate fertilization would then practically never occur in nature, especially in a form so frequently visited by insects. H. MÜLLER records (**28,** p. 165) 41 species of insects seen on the flowers of the buckwheat, many of them very frequently.

It is entirely possible that the rate of growth of the pollen tube was more rapid under the conditions of the experiment than it is in nature, for the temperature of the greenhouse in which the plants were grown was rather high. It does not seem probable, however, that this would affect the relative rate of growth of the pollen tube in the two cases.

THE REDUCTION DIVISION OF THE POLLEN MOTHER CELLS

Each loculus contains usually a single row of 8 or 10 pollen mother cells. All the cells of each loculus apparently pass through the different stages simultaneously, and there is no evidence of a regular basipetal succession in their development, such as has been reported in numerous cases. It was necessary, therefore, in order to determine the succession of the various stages, to compare carefully the cells of different loculi, using their size and the condition of their cytoplasm as a check upon the order of the phases shown by the nuclei. Considerable variation in different loculi of the same flower is common.

PROPHASE.—The pollen mother cells first become distinguishable by their increased size and the possession of a large nucleus, containing a single large, dark staining nucleolus (figs. 1, 2). This nucleolus is surrounded by a clear zone which is apparently not affected by any of the stains used. In a few cases two such nucleoli were observed in one nucleus, each surrounded by the colorless area just described. The nature of this clear space seems to be rather uncertain. It has been figured frequently, and is regarded by some writers as a constant structure. MARTINS MANO (**24**, p. 60) speaks of it as the "peri-nucleolar vacuole." STRASBURGER, however, considers that the appearance is due to reagents (**37**, p. 519).

Surrounding this clear zone is the nuclear reticulum, consisting of very delicate indefinite threads which do not take the chromatin stain. This "linin" network contains scattered dark staining bodies which are apparently rather irregular in number and do not seem to occur in pairs. They thus furnish no support for the attractive prochromosome theory of ROSENBERG (**31**, p. 25) and others.

SYNAPSIS.—The recent work of LAWSON (**22**) has again raised the question as to whether the phase of the nucleus preceding the reduction division, characterized by an apparent condensation and contraction of the chromatin on one side of the nuclear cavity, is a real contraction. For some time this condition was regarded as an artifact, but it has been observed in living material by several investigators, and its occurrence, at least in some forms, is now

generally admitted. Some writers, however, still regard it as due to imperfect fixation.[1] This stage was first called "synapsis" by MOORE in 1895; and many cytologists have come to regard it as an important and critical stage, when the actual fusion of the maternal and paternal chromosomes occurs.

LAWSON presents a different explanation of the condition observed. He interprets the phenomenon as simply a growth period of the nucleus, during which the increased osmotic pressure within the nucleus causes the absorption of a considerable amount of cell-sap, and the consequent increase in size of the nucleus. In this enlargement the chromatin mass is left behind. The characteristic position of the chromatin mass at one side of the nucleus, according to LAWSON, is due to the fact that the extension of the nuclear cavity always takes place in one direction, that is, on the side toward an intercellular space where there is least resistance from the neighboring cells.

Since the publication of LAWSON's paper, the writer has studied the synaptic stages in the buckwheat with special reference to the comparative size of the nucleus and chromatin mass before and during synapsis. There is certainly an increase in the size of the nucleus during the synaptic stages, as will appear from a comparison of figs. 3, 4, and 5. It seems equally certain that the chromatin mass occupies a much smaller space during the "balled-up" condition than it does either before or after this stage. The stage is evidently of considerable duration, longer than all the later stages in the heterotypic division combined.

It is of course possible that the contraction is due to imperfect fixation, that the nuclear matter is for some time in such a condition that it is impossible to preserve its structure by any known method. A contraction at this stage, however, is of constant occurrence, and the chromatic material has a characteristic appearance after the "contraction" which differs markedly from its appearance before. The same conditions were found in *Houstonia;* and in the following descriptions it will be assumed that synapsis is a normal stage.

A comparison of the nuclei before and after synapsis is rendered

[1] A full discussion of this subject, together with citations of literature, is given by GRÉGOIRE (17, pp. 332–335).

easier by a change which takes place in the cell at this time, and by which postsynaptic stages are clearly distinguished from presynaptic stages. During the contracted condition of the chromatic mass the pollen mother cell becomes rounded and takes on a more spherical form. In figs. 3, 4, and 5, the nuclei are apparently in much the same stage, but the cells show a progressive "rounding off." Such a change in the shape of the cell during synapsis has been observed by STRASBURGER, ALLEN (**1**, fig. 19), DAVIS (**12**, p. 634), and others, and appears in the figures of many workers who make no particular mention of it.

The synaptic contraction seems to take place by a drawing together, at one side of the nucleus, of the whole nuclear reticulum, usually but not always including the nucleolus (figs. 3 and 5). On careful examination this mass appears to consist, at least in part, of delicate threads; but no evidence of any pairing of these threads, such as has been described by some investigators, could be obtained. The threads of the nuclear reticulum in the buckwheat are so delicate, however, that it would be extremely difficult to demonstrate any such condition even if it occurred; and the behavior of the chromatin at later stages makes it seem probable that a pairing has actually taken place at this stage.

The amount of chromatin staining material is very markedly increased during synapsis. Before the contraction, the greater part of the reticulum does not take the chromatin stain; but the nuclear mass comes out of the contracted condition as a series of rather thin loops (fig. 7), each of which consists, apparently, of a single thread which takes the chromatin stain uniformly throughout its length. This thread is granular in appearance and varies somewhat in thickness; but no alternation of chromatic and achromatic material, such as has been described by some writers at this stage, could be made out. The number of loops is rather inconstant, but is generally greater than the number of gemini.

These loops gradually shorten and thicken (fig. 8) and become more dense and uniform in appearance. At the time of greatest thickness they undergo a longitudinal split (fig. 9), thus giving rise to a series of paired chromatic threads from which the gemini are apparently formed by the continued gathering together of the

chromatic material. The stages from the loosening of the synaptic knot to the formation of the gemini are passed through rather rapidly; and the changes apparently take place in all parts of the nucleus at practically the same time. There does not seem to be any definite "second contraction," but rather a continuous shortening and thickening of the threads from the time the thin loops first appear until the gemini are formed.

The two members of a geminus are generally united at one end, but they are often found entirely separate or united throughout their length (figs. 11 and 12). Their appearance in figs. 10 and 11 would indicate that the loops from which they arose consisted of both chromatin and linin, and that in the formation of gemini at least a part of the linin is discarded. Diakinesis is apparently of considerable duration and affords an excellent opportunity for counting the chromosomes. The reduced number is evidently 8. The nucleolus appears at this stage as a pale and somewhat irregular body (figs. 10–12).

The succeeding stages present no unusual features. The first division separates the two members of the gemini, but there is no evidence of a longitudinal split in the chromosomes during the anaphase (fig. 13). During interkinesis the daughter nuclei of the first division approximate somewhat a resting condition. A rather definite nuclear membrane is formed, a pale nucleolus appears, the chromosomes become more or less vacuolate, and are connected to some extent by indefinite linin threads (fig. 18). It is usually possible at this stage, however, to make out the separate chromosomes and to determine definitely the reduced number, 8. The second division is a typical homotypic division.

It will be noted that the condition described for the buckwheat corresponds closely with the "hétérohoméotypique scheme" of GRÉGOIRE (**17**, p. 233). His "scheme" may be briefly outlined as follows: In the early prophase (p. 243) of the reduction division, the nuclear mass becomes resolved into a number of fine threads, each of which is the equivalent of a somatic chromosome. This is the leptotène stage. These threads, the "gamomites," become arranged in pairs (zygotène stage), which afterward fuse to form a series of independent loops, the pachytène loops. These pachy-

tène loops exist in the haploid number, and soon undergo a longitudinal division, which is really the separation of the parts which united in their formation. The halves thus separated often appear irregularly spread apart and crossed, the "strepsitène" stage; and the "gemini" are formed by the shortening and thickening of these strepsitène loops. Diakinesis (p. 232) is characterized by the presence of "chromosomes" in the reduced or haploid number, formed often of two rather independent branches. The first division separates the two branches of these "chromosomes," and the daughter chromosomes show during the anaphase of the first division a longitudinal split, which is sometimes visible in the two branches of the diakinetic "chromosomes." After an interkinesis, more or less brief, marked by varying degrees of nuclear reconstruction, the daughter chromosomes of the first division reappear, and their longitudinal halves are separated in the second division.

In GRÉGOIRE's scheme, synapsis, when it occurs, is due to the contraction which accompanies the fusion, in pairs, of the leptotène threads to form the pachytène loops. If this change takes place simultaneously throughout the nucleus, a crowding of the whole chromatin mass at one side is the result.

If it is assumed, as seems probable, that in the buckwheat a fusion of thin filaments takes place in the presynaptic stages, then the series of loops characteristic of the early postsynaptic period represents a pachytène stage. There are, however, considerably more than the haploid number of loops. This may mean either that the loops representing the chromosomes are long (GRÉGOIRE, p. 335) or that they are parts of a continuous spirem thread. These two explanations represent the two interpretations of the spirem condition, STRASBURGER and his school maintaining that the chromatic mass comes out of synapsis as a continuous spirem thread, GRÉGOIRE holding that the so-called spirem is really a series of independent loops. On this point the buckwheat furnishes no evidence. It seems certain, however, that these loops become shortened and thickened and undergo a longitudinal split, forming the strepsitène loops, from which the gemini are derived by a continued thickening.

It was also noted above that no split in the chromosomes is evident in the anaphase of the first division. But though such a split is stated by GRÉGOIRE to be a part of his "scheme," its absence cannot be regarded as a very important deviation.

THE CHROMOSOMES IN THE REDUCTION DIVISION

As the chromosomes become vacuolate during interkinesis, the stage most favorable for an examination and comparison of the chromosomes is the anaphase of the reduction division (fig. 13). The most striking thing about the chromosomes at this stage is their different size in the two forms. The chromosomes of the short-styled form have a diameter nearly twice as great as do those of the long-styled form (compare figs. 14 and 15 with figs. 16 and 17). As it is entirely improbable that this difference in size can be due to any difference in the hereditary qualities borne by the two sets of chromosomes, it appears to be related with the corresponding, though smaller, difference in the size of the microspore mother cells at this stage.

Just what relation exists between the size of the cell, the size of the nucleus, and the size and mass of the chromosomes is not well understood. There seems, at any rate, to be no definite relation between the number of chromosomes and the size of the nucleus. STRASBURGER (**36**, p. 51) cites several cases in which the nuclei with the diploid number of chromosomes are distinctly larger than those with the haploid number in the same species. In the seed rudiments of *Taxus baccata*, for example, the nuclei of the prothallium are much smaller than those of the nucellus. That the diploid number of chromosomes is not always associated with a larger nucleus than that which contains the haploid number, however, he proves by the case of *Dictyota dichotoma*, in which species the nuclei of the plants which produce tetraspores are no larger than those of the plants which bear eggs or sperms, though they have, of course, twice as many chromosomes.

Another difference between the two forms, which is apparently constant, is the arrangement of the chromosomes in the anaphase of the heterotypic division. In the short-styled form the eight chromosomes tend to be arranged with six in the peripheral ring

and two in the middle; while in the long form the arrangement shows seven in the periphery and one in the middle. This arrangement may of course be accidental or it may be mechanical, due to the difference in the chromosomes (compare figs. 14 and 15 with figs. 16 and 17).

A careful examination of the cells in the late anaphase of the heterotypic division of the short-styled form failed to show any difference in the chromosomes (figs. 14 and 15). In the long-styled form, however, the "central" chromosome is apparently considerably larger in one of the daughter nuclei of the heterotypic mitosis than is its synaptic mate in the sister nucleus (figs. 16 and 17). While this condition is apparently constant, little importance can be attached to it until more is known of the inheritance of heterostyly in the buckwheat,[2] and of the reduction division of the megaspores. It bears a striking resemblance, however, to the condition found in the sperm mother cells of *Lygaeus* and other insects (WILSON, **40**, p. 59) in which there is an "x" chromosome which has as a synaptic mate a smaller "y" chromosome.

GROWTH OF THE POLLEN MOTHER CELLS

The difference in the size of the pollen grains of the two forms has been referred to above. As a corresponding difference in size was apparent in the pollen mother cells during early stages, an examination was made to determine whether a similar difference in size occurs in the somatic cells. Buckwheat seeds were allowed to germinate on moist filter paper, and when the roots were about half an inch in length the tips were removed with a sharp razor and fixed at once. Seeds and root tips were carefully marked to correspond and the seeds planted.

The seedlings developed readily, and when the plants blossomed, microtome sections of the root tips were prepared and the size of the embryonic cells of the two forms compared. The cells measured, of course, were always in the same stage, usually the metaphase. Some variation in the size of the embryonic cells even in the same stage was noted, but no constant difference between the two forms

[2] DARWIN's experiments on this species, as he himself states, were and gave the result that illegitimate seeds of either form produced pl

could be demonstrated. No difference is apparent either in the resting nuclei of the pollen mother cells or in the pollen mother cells themselves (figs. 1 and 2). The difference becomes evident, however, after the rounding off of the pollen mother cells during synapsis, and apparently reaches its maximum some time before diakinesis, (compare figs. 7 and 8; and figs. 11 and 12). It is of course much easier to measure accurately spherical cells than angular cells massed together, as it is extremely difficult to determine in the latter case whether the cells are cut in the same plane or not, and there may be a difference in the size of the somatic cells which could not be determined. It seems entirely probable, however, that the difference in the size of the pollen of the two forms is due to the fact that the pollen mother cells of the short-styled form grow more rapidly during the period from the beginning of synapsis to diakinesis, than do the microspore mother cells of the long-styled form. It is interesting to note in this connection that it is during this same period that the ovocyte in animals undergoes its greatest enlargement (GRÉGOIRE, **17**, p. 243).

SEPARATION OF THE POLLEN GRAINS

The separation of the pollen grains occurs in much the same way as was described by Miss FERGUSON for *Pinus* (**14**, p. 35). During the late telophase of the second mitosis in the microspore mother cell the four nuclei of the tetrad become connected with one another in all directions by "kinoplasmic" fibers (fig. 19). These fibers, however, are never very numerous, and they are visible for only a comparatively short time after the reconstruction of the daughter nuclei is complete. During this period a marked thickening of the wall of the pollen mother cell occurs (fig. 20); and, apparently continuous with this wall and extending out from it, walls appear separating the daughter cells (fig. 21).

These walls attain a remarkable thickness, and are apparently homogeneous and extremely resistant to stains. They stain very lightly with haematoxylin or safranin, and with orange G only if the staining be considerably prolonged. The strength and definiteness of the walls thus formed is shown by the fact that after the spores are mature and the wall of the mother cell is ruptured, the

empty mother cell wall with its four chambers often persists for some time (fig. 22).

TAPETAL CELLS

About the time the pollen mother cells reach the pachytène stage, the tapetal cells begin a rather irregular free nuclear division. The nuclei show all gradations from true mitosis to what is apparently simple amitotic division. Figs. 23–25 show the amitotic division of these nuclei. By the time the pollen mother cells have finished the homotypic division, the tapetal cells regularly contain two and sometimes four free nuclei (fig. 26).

MEGASPORE MOTHER CELLS

The difficulty of orienting the buds makes the number of preparations necessary to secure a full series of stages so great that a complete study of the development of the megaspores has not yet been made. One preparation of the long-styled form, however, showed typical diakinesis, which, as was to be expected, had much the same appearance as that in the microspore (fig. 27). Usually only one megaspore mother cell is formed in an ovule, and each flower produces but a single seed. One ovule, however, which happened to be in the long-styled form, contained two apparently well-developed and normal megaspore mother cells, with their nuclei in the pachytène stage. Their shape seems to indicate that they were formed by the division of a single cell by an anticlinal wall (fig. 28).

Houstonia caerulea

The Rubiaceae contain nearly half the genera known to be heterostylous. The flowers of *Houstonia* are plainly dimorphic, the pistil being exserted in one form and the stamens in the other. The pollen grains vary somewhat in size in each form, but those of the short-styled form are larger than those of the long-styled, their diameters being in about the ratio 10:7. No differences have been noted in the vegetative structures of the two forms. The flowers are so small that experimenting with them would be very difficult, and accordingly very little is known about the relative fertility of legitimate and illegitimate unions. DARWIN, however (11, p. 132),

observed that some short-styled plants growing by themselves at a considerable distance from any long-styled plants produced mostly sterile capsules. From this he concludes that the short-styled form is very sterile with it own pollen.

The pollen mother cells are small and a large number are contained in one loculus, often as many as 40 appearing in a single longitudinal section. Considerable variation is generally shown by the cells of a loculus, but there does not seem to be any very regular succession of stages. Frequently, to be sure, an anther shows a progressive series with the most advanced stages at the top; but this is by no means a uniform condition, for occasionally a loculus shows the mother cells near the middle in a more advanced condition than the cells at either end. The relative position of the cells in an anther does not, then, in *Houstonia*, furnish reliable evidence of the succession of the stages. This makes the exact significance of some stages rather uncertain, and some of them are open to more than one interpretation.

THE REDUCTION DIVISION OF THE POLLEN MOTHER CELLS

PROPHASE.—The pollen mother cells first become distinguishable by their increased size and the possession of a very large nucleus. The nuclear reticulum appears as a network of very fine irregular threads, and contains numerous granules, none of which take the chromatin stain. There is usually only a single large nucleolus, and this is surrounded by the clear zone already described in the buckwheat.

The nuclei of the pollen mother cells present at this stage an appearance which has been variously interpreted. Figs. 29–33 show what appears like a progressive "budding off" of chromatin staining material from the nucleolus. A similar condition has been observed by DARLING (**5**, p. 184) in *Acer Negundo*, and described as a budding off of actual chromatin which goes to make up the spirem thread. Miss NICHOLS (**30**, p. 35) has observed this condition in *Sarracenia*, and considers that it represents a movement of chromatin, which has been elaborated in the nucleolus, to the nuclear reticulum. GATES (**15**, p. 6) interprets a similar appearance in *Oenothera* in an entirely different manner. He regards the

dark staining bodies in the nuclear reticulum as small nucleoli, and thinks that conditions similar to those in figs. 30, 32, and 33 represent a fusion of some of these smaller nucleoli with the large one.

As it is impossible to arrange these stages in *Houstonia* with any certainty, there is no proof as to what actually takes place. The appearance strongly suggests a "budding off" of material which is caught up by the nuclear reticulum; and the presence of numerous dark staining bodies in the reticulum at the time of synapsis (figs. 34 and 35) have been held to show that such is actually the case. There is no proof, however, that the dark staining bodies which are present in the reticulum at this time have any connection with the nucleolus. In fact, a series of somatic stages, taken from the rapidly growing tissue of a young ovule (figs. 36–42), seems to show that the dark staining masses appearing in the reticulum previous to the formation of the spindle have no connection, at least directly, with the spherical bodies observed near the nucleolus, but that they are chromosomes which become differentiated from the nuclear reticulum during the prophase.

SYNAPSIS.—Synapsis is characterized by a crowding together at one side of the nucleus of the entire nuclear reticulum (figs. 34 and 35). No structure can be made out in this mass except that it consists of a number of dark staining bodies in a much lighter, rather indefinite network. Synapsis is of considerable duration, and during this period the nucleus undergoes a marked increase in size (compare figs. 34 and 35) and the cell becomes rounded (fig. 43).

SPIREM STAGE.—The chromatic mass comes out of synapsis in a series of thin loops (figs. 43 and 44). Each loop apparently consists of a single thin thread which does not take the chromatic stains uniformly throughout its length, but shows numerous dark staining bodies, connected by paler linin portions. As these loops shorten and thicken they stain more uniformly (fig. 45).

The synaptic knot loosens very slowly, and even at the period of greatest thickening of the loops there is still a considerable portion of the nuclear mass, which does not show any definite structure, surrounding the nucleolus (fig. 45). This condition can be explained only on the supposition that some parts of the nucleus often pass

through the various stages in advance of others, a condition comparable to that noted by JANSSENS (21) in *Batracoseps*. The appearance at later stages seems to bear out this supposition. Fig. 46 shows a split in a portion of the spirem, while the rest appears entirely undivided. Fig. 47 shows several places where the parts have become still more widely separated, yet a considerable mass of the nuclear material is still in synapsis; and fig. 49 shows all gradations from paired loops to typical gemini.

This irregularity in development, together with the fact that there is no definite succession of stages in the loculi, makes a fully satisfactory interpretation of the spirem stages impossible. If it is true, however, as seems probable, that the chromatic loops which appear as the mass emerges from synapsis consist of a single thread[3] which afterward shortens and thickens, and if the split shown in figs. 46 and 47 represents a separation of threads previously paired, the series accords closely with GRÉGOIRE's hétérohoméotypique scheme. Figs. 44 and 45 would then represent the pachytène stage, the loops shown in fig. 45 resulting from a shortening and thickening of thinner loops shown in fig. 44. Fig. 46 doubtless represents a splitting of the pachytène loops, the diplotène stage. Figs. 47 and 48 show different stages in strepsinema; in fig. 47 only a small part of the nuclear mass is in the strepsitène condition, while fig. 48 is a more advanced stage.

The appearance of fig. 43, which is quite characteristic of the loosening of the synaptic knot, makes it appear possible that the spirem comes out of synapsis as a series of paired threads which afterward fuse to form a continuous spirem. That this actually occurs in most cases is held by STRASBURGER and his school. Such a condition as is shown in fig. 44, however, where the loops appear still thin but with the halves widely separated, makes it seem probable that the thickened spirem arises from the thinner by a thickening of the threads. That is, figs. 44 and 45 represent merely different phases of the pachytène stage.

[3] In referring to this stage as characterized by the occurrence of loops consisting of a single thread, the writer does not mean to enter into the discussion as to whether this "single thread" is really a unit or is composed of two separate threads twisted together. The expression "single thread" is used to mean simply a loop which appears as one thread, as distinguished from one composed of two parallel threads.

DIAKINESIS.—In either case the diakinetic gemini arise by the continued shortening of the paired loops which make up the strepsitène stage. As shown by fig. 49, diakinesis may not arise simultaneously throughout the nucleus. The stage is of considerable duration, however, and presents a very characteristic appearance (figs. 50 and 51). The chromosomes of a geminus are generally united only at one end and often diverge widely from one another. The nucleolus at this stage appears vacuolate, and shows in section an outer dark staining region surrounding an inner almost colorless portion. Commonly at this stage one or two gemini appear clinging to the nucleolus (fig. 51). Their appearance suggests the condition reported by DARLING (**5**, p. 186) for *Acer Negundo*, where five chromosomes appear to arise directly from the nucleolus. There is nothing in *Houstonia*, however, to indicate that this condition is anything more than a clinging of the gemini to the nucleolus.

Another characteristic appearance during diakinesis is that shown in figs. 52 and 53, where several gemini appear clinging together in a single row. This condition very much resembles that found by GATES (**15**, p. 12) in *Oenothera*. GATES, however, considers that in *Oenothera* this condition is previous to true diakinesis, and represents a single continuous spirem constricted at regular intervals to form a chain of chromosomes. Some of these chromosomes afterward pair to form typical gemini, but a considerable number of them are apparently taken up by the heterotypic spindle without having previously paired. An essentially similar method of formation of the diakinetic chromosomes has been reported by GEERTS (**16**, p. 610) and by Davis (**12**, p. 559) for *Oenothera*, and by YAMANOUCHI (**41**, p. 186) for *Fucus*.

That such is the case in *Houstonia*, however, seems improbable, as such an interpretation makes it necessary to regard the condition shown in figs. 46 and 47 as a precocious split which afterward closes up. Moreover, the two members of each geminus in *Houstonia* are almost always found attached at one end, while in *Oenothera* such a condition is the exception. The condition shown in figs. 52 and 53 seem to be best explained as a temporary union of independent gemini, an interpretation first suggested by MIYAKE (**25**, p. 96) for a similar appearance in *Galtonia candicans*.

INTERKINESIS.—The heterotypic division presents no unusual features, but interkinesis differs markedly from that of the buckwheat. Although a rather definite nuclear membrane is formed, the chromosomes show no signs of vacuolation or anastomosis. On the contrary, they become arranged around the periphery of the nucleus and present at this stage the most satisfactory opportunity for counting and comparing the chromosomes (figs. 57 and 58). The haploid number is 16.

Nucleoli appear at this stage and stain with haematoxylin in exactly the same way as the chromosomes themselves; in fact they were at first mistaken for larger, more regular chromosomes. With safranin, however, the nucleoli are clearly differentiated from the chromosomes. There may be either one or two nucleoli at this stage, but sister nuclei seem to agree in this respect, that is, if one daughter nucleus of the first division shows one nucleolus, its sister nucleus also has only one, but both may, on the other hand, have two nucleoli (figs. 57 and 58). This peculiarity seemed at first to bear out the idea that they were chromosomes, and there seems to be a constant difference between the two forms, the long-styled form having two nucleoli (fig. 58) and the short-styled form one larger nucleolus (fig. 57). This may possibly be due to the different sizes of the nuclei in the two forms.

THE CHROMOSOMES IN THE REDUCTION DIVISION

Interkinesis, because the chromosomes remain apparently unchanged and are arranged in the periphery of the nucleus, affords the best opportunity for comparing the chromosomes of the reduction division. No difference in the chromosomes that enter into the formation of the daughter nuclei could be discovered. In fact, both in interkinesis and in the anaphase of the reduction division the chromosomes show very little variation in size. A constant difference in size between the chromosomes of the long-styled and short-styled forms is evident in the anaphase, but this is much less marked than in the buckwheat (compare figs. 55 and 56).

RELATIVE SIZE OF THE POLLEN MOTHER CELLS

The pollen grains of the two forms differ fully as much in size as do the two forms in the buckwheat, but the difference does not

seem to appear so early in their development. The fact that the cells are small and vary somewhat in size makes it difficult to determine when the difference becomes most pronounced; but it will be clear from a comparison of the figures that at diakinesis, the heterotypic division, and the formation of the tetrad, some difference in size is evident. Compare figs. 50 and 51, 55 and 56, and 59 and 60.

SEPARATION OF THE POLLEN GRAINS

The daughter nuclei of the homotypic division show at an early stage a nucleolus similar in staining reactions to that of interkinesis (figs. 59 and 60). That is, the nucleoli stain with hematoxylin exactly the same as the chromosomes, so that in early stages of nuclear formation it is impossible to distinguish them, and the nucleolus appears to arise by a fusion of the chromosomes. Staining with safranin, however, shows clearly that the nucleolus arises separately, but increases in size as the chromosomes lose their staining capacity.

The separation of the pollen grains takes place in much the same way as in the buckwheat, except that in *Houstonia* the "kinoplasmic" fibers connecting the nuclei of the tetrad are much more clearly marked and persistent. The walls which surround the mother cells and separate the cells of the tetrad are not so thick or resistant as in the buckwheat.

Summary of observations

Fagopyrum esculentum

The flowers, as a rule, are true to form, but occasional "equal-styled" flowers are found on both long-styled and short-styled plants. None of these "equal-styled" flowers have been proved to be fertile.

In the case of legitimate pollination less than 18 hours is required for the growth of the pollen tube and the fusion of the egg and sperm nuclei. Illegitimate fertilization is possible, at least in part of the cases; but in case of illegitimate pollination more than 72

hours is necessary for the growth of the pollen tube and the fusion of the nuclei.

No evidence of prochromosomes was found in the pollen mother cells.

The formation of the gemini and the reduction division apparently follow the hétérohoméotypique scheme of GRÉGOIRE; but no split in the chromosomes is evident in the anaphase of the first division.

The reduced chromosome number is 8.

In the anaphase of the reduction division of the microspore mother cells the chromosomes of the short-styled form have a diameter nearly twice as great as do those of the long-styled form.

At this stage the chromosomes of the short-styled form are arranged six in the peripheral ring and two in the middle; while those of the long-styled form are arranged seven in the periphery and one in the middle.

In the long-styled form the "central" chromosome of one of the daughter cells of the first division appears to be larger than its synaptic mate.

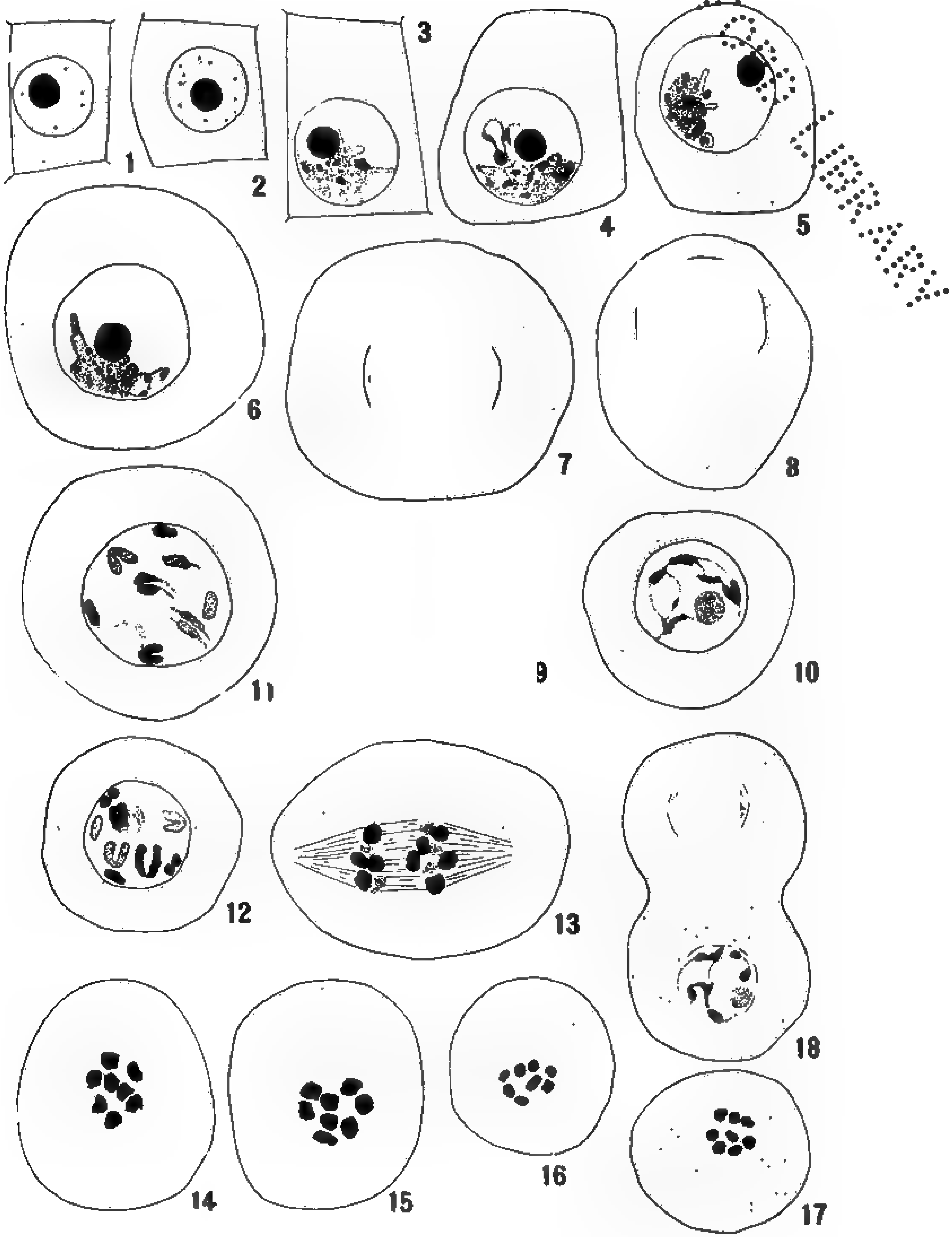
Interkinesis is characterized by a partial reconstruction of the nuclei, a nucleolus appears, and the chromosomes become somewhat vacuolate but never lose their identity.

A difference in size of the pollen mother cells of the two forms, corresponding to the difference in the size of the pollen grains, is evident at diakinesis. This difference apparently arises through the greater growth of the pollen mother cells of the short-styled form up to this stage, for no difference in the size of the somatic cells can be found.

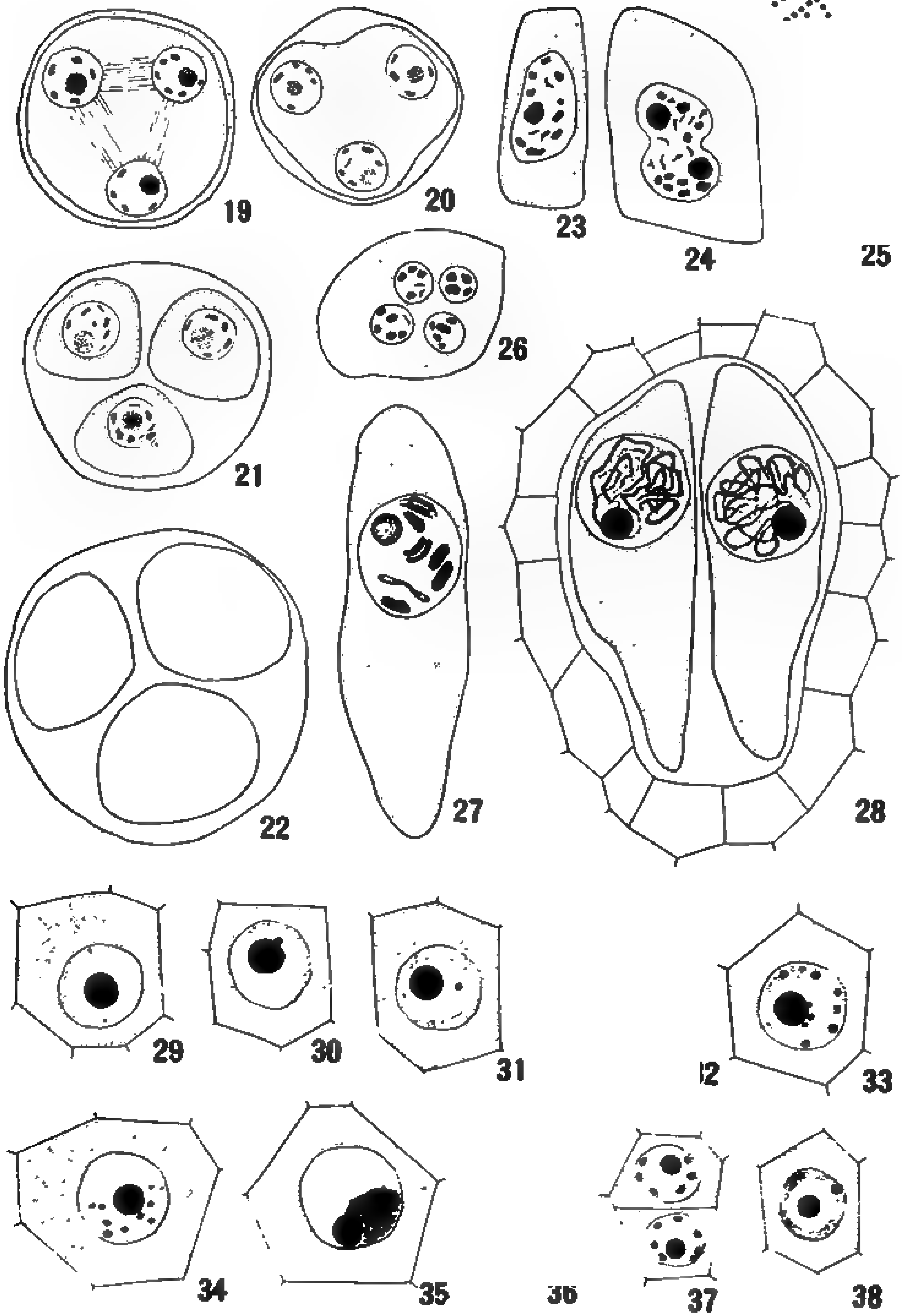
At the separation of the cells of the tetrad a thick wall, apparently homogeneous and extremely resistant to stains, is formed surrounding the pollen mother cells and separating the pollen grains.

As the tapetal cells degenerate, they show free nuclear division which is to some extent at least amitotic.

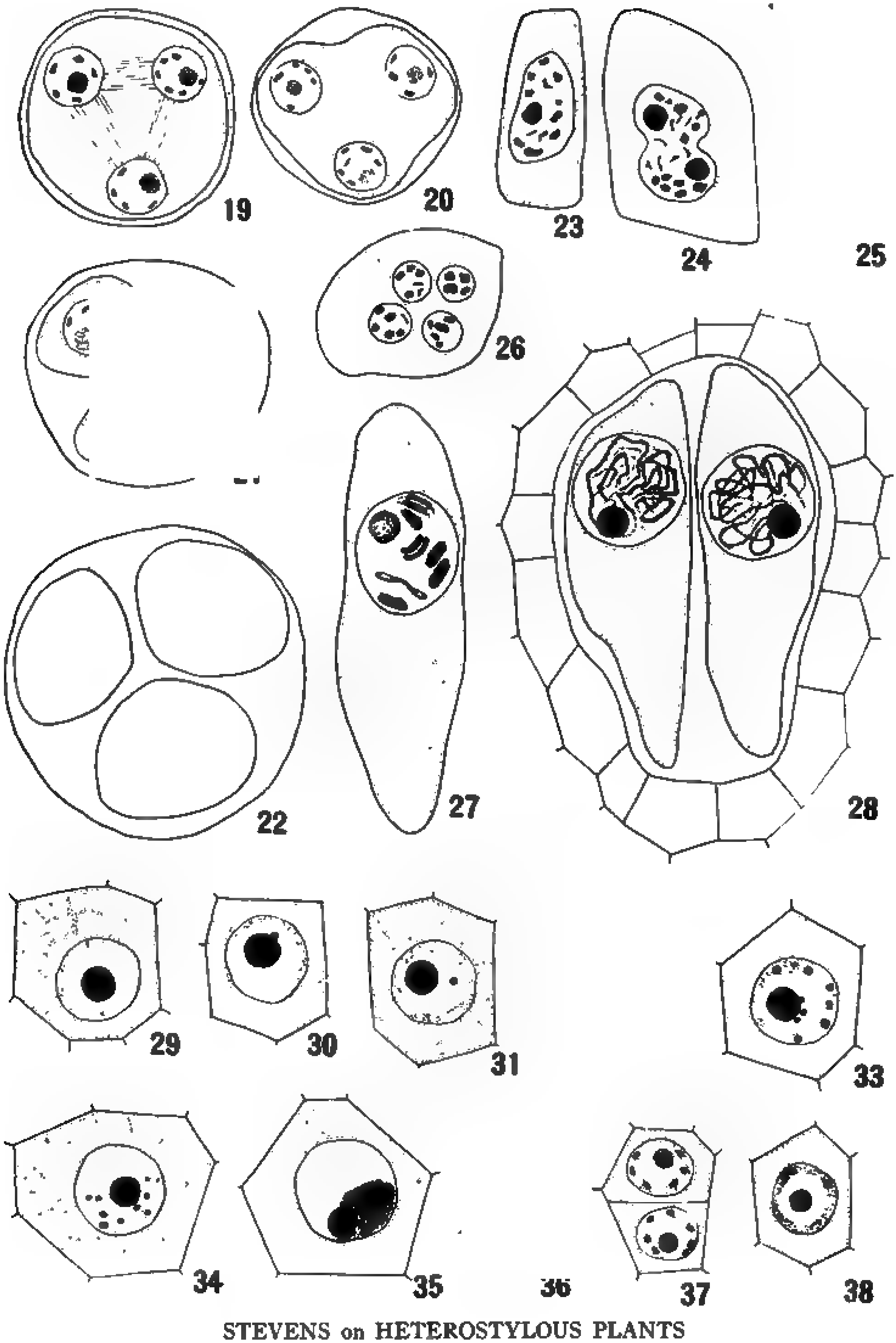
Usually only one megaspore mother cell is formed in an ovule, but one ovule was found which showed two well-developed megaspore mother cells. These had apparently arisen by the longitudinal division of a single cell.



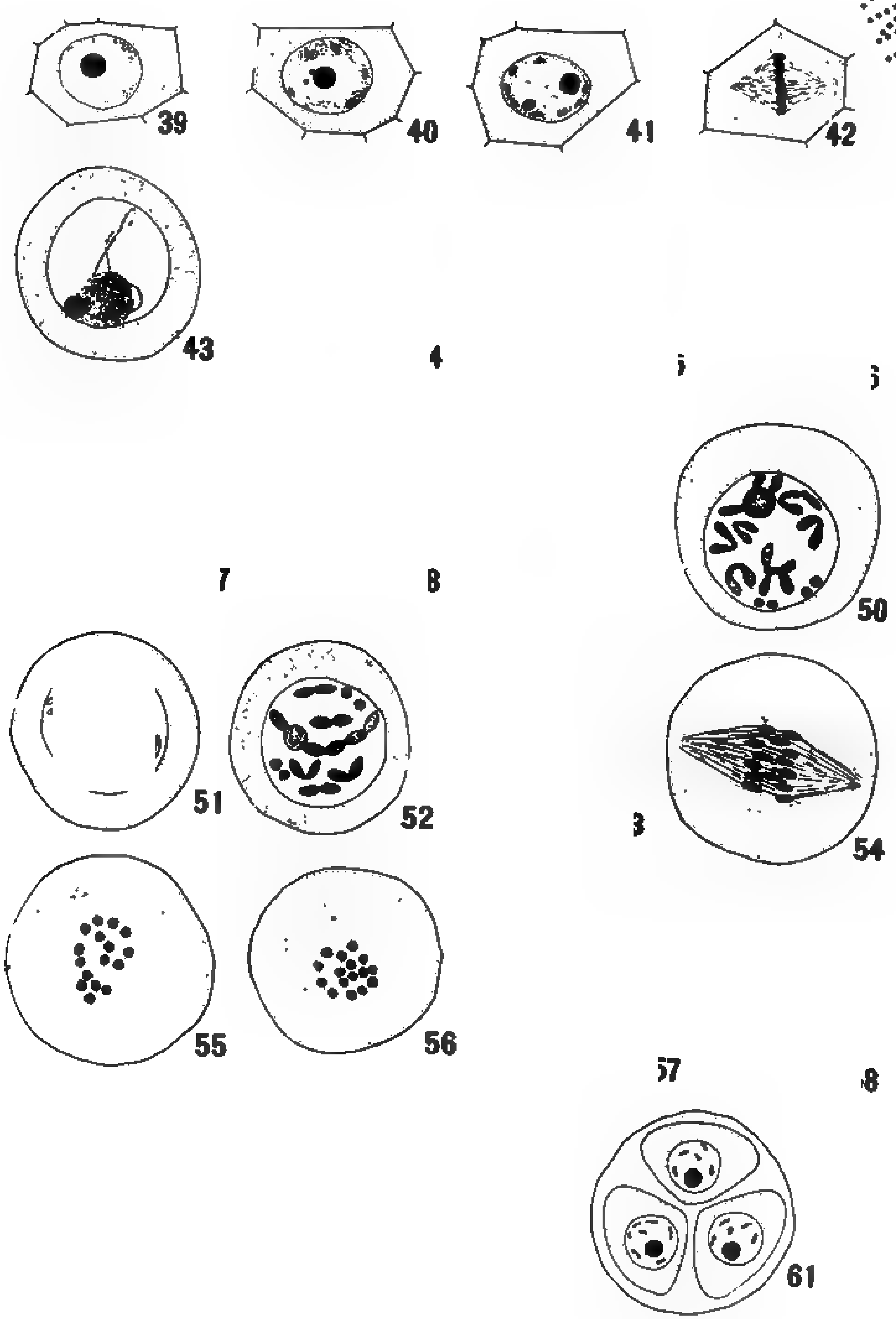
STEVENS on HETEROSTYI[illegible]TS



STEVENS on HETEROSTYLOUS PLANTS



STEVENS on HETEROSTYLOUS PLANTS



PLANTS

RELATION OF THE DAILY MARCH OF TRANSPIRATION TO VARIATIONS IN THE WATER CONTENT OF FOLIAGE LEAVES

BURTON EDWARD LIVINGSTON AND WILLIAM HENRY BROWN[1]

Introduction

As was first pointed out in Publication 50 of the Carnegie Institution (1906), it is only by correcting the variations in the transpiration rate to uniform conditions of evaporation (that is, to a uniform evaporating power of the air), that anything approaching quantitative information concerning the seemingly almost autonomous changes in the rate of water loss from plants may be had. To accomplish this correction it is only necessary to consider the march of the ratio of the rate of transpiration to that of evaporation, the latter determined by means of some form of atmometer. This ratio has been termed *relative transpiration;* it denotes simply *the number of atmometers of the form used that would be necessary to evaporate the same amount of water as is lost by the transpiring plant in the same time and at the same place.* In other terms, relative transpiration is a measure of the equivalent or effective evaporating surface of the plant as this varies from time to time, the unit of evaporating surface being unit area of free water surface under properly defined conditions, or any other evaporating surface which may be adequately defined. √

Reference to the nine graphs of relative transpiration presented in the publication just mentioned, and to the accompanying discussions, brings out the fact that the maximum of the evaporating power of the air (the evaporation rate from the porous cup atmometer in this instance) always occurred, in the cases cited, somewhat later in the day than did the maximum of relative transpiration (the ratio of transpiration rate to that of evaporation). This was

lace in

ile the

Such

postulated change would not necessarily result in a decrease in the actual rate of water loss, thus forming a maximum point in the graph of *absolute* transpiration, but might merely *retard the increase* in this rate and thus give that graph a *lower slope* as it approaches its later-occurring maximum. The graph of *relative* transpiration, however, should show a definite maximum at the point when this retarding change was applied, since this graph is entirely independent of the direct effects of variations in the evaporating power of the air.

The maximum of absolute transpiration might occur at the same time as that of relative transpiration (when the postulated retarding influence may be considered as of greater magnitude than the accelerating influence of the still increasing evaporating power of the air), or it might occur later (when the acceleration due to the increasing evaporation rate may be considered as of greater influence than is the internal retardation). In fig. 8 of the publication to which we are referring, two of these maxima in the graph of absolute transpiration ("Rta") occur simultaneously with maxima in relative transpiration, while another occurs later than that in relative transpiration but earlier than the maximum in the graph of evaporation. The first two cases fulfil the former and the third the latter of the two suppositions made above.

In seeking to examine this daily retardation somewhat more closely, it was found (Publ. 50 still) that the maximum in relative transpiration thus evidenced might occur at almost any hour before the evaporation maximum, but that its occurrence usually fell in the hours between 10:00 A.M. and 1:00 P.M. This maximum, furthermore, appeared to be related to temperature. "As far as the limited data at hand can be trusted, the temperature of the surrounding air seems to be the controlling condition which governs this regulative response. . . . . There is some evidence that intensity of evaporation is the controlling factor, in some cases at least."[2]

From eleven cases on the graphs of the contribution just cited, we have calculated the amount of decrease in relative transpiration

[2] LIVINGSTON, B. E., The relation of desert plants to soil moisture and to evaporation. Publication 50 of the Carnegie Institution, 1906, pp. 63–64.

which was manifest at the time of the evaporation maximum. Thus, at its maximum, the relative transpiration ratio of *Euphorbia* (Publ. 50, Carnegie Inst., fig. 8) is 0.069, this ratio falling rapidly and becoming only 0.035 at the time when the highest evaporation rate for the day is reached. Thus, during the period indicated the retardation of relative transpiration has amounted to 50.8 per cent. On the second day this retardation amounts to 33.3 per cent. The average percentage decrease for the eleven cases is 48.6 per cent, there being little variation in the terms of the series (33.3 is the smallest, the next higher is 41.8, and the largest is 61.2), and we may conclude that the retardation in water loss, for this period, is about 49 per cent. It is improbable that there occurred any closing of stomata during the period involved in this calculation, for the maximum in the evaporating power of the air always occurred long before sunset. Indeed, the retardation which is manifest before any stomatal closing is to be expected is of a considerably higher magnitude than that taken in our calculation, so that the average value of this retardation is surely somewhat greater than that given here.

With this approximation of the magnitude of the internal retardation of water loss, and with the above observation as to its time of occurrence in the day (10:00 to 1:00), we may attempt to ascertain what may be its probable cause.

Preliminary considerations

(1) Incipient drying

In some recent studies[3] bearing upon the quantitative relation between the intensity of sunlight and transpiration, it has been emphasized more than heretofore how important an accelerating influence sunshine may exert upon the rate of water loss from green plants. This influence of solar intensity upon transpiration rate led the writer of the paper last cited to suggest that the internal retardation in water loss which occurs prior to the maximum rate of

[3] Livingston, B. E., (1) Light intensity and transpiration. Bot. Gaz. 52:417–438. 1911.

———, (2) A radio-atmometer for comparing light intensities. Plant World 4: 96–99. 1911.

evaporation for the day may be due largely to an increase in the rate of *water loss itself*, as this may be brought about by a rise in the air temperature and especially by absorption of solar energy. This supposition has the appearance of a paradox, since the acceleration of a process is postulated as causing a retardation of the same process, but such phenomena are not infrequent where disturbances in the equilibrium of a system are dealt with, and the suggestion seems worthy of careful theoretical and experimental consideration.

On purely a-priori grounds it is readily understood from the principles of thermodynamics, that a rise in the temperature of the air which bathes the leaves (such as normally progresses throughout the forenoon and well into the afternoon) should produce an ever-increasing vapor pressure of water within the internal atmosphere of the foliar tissues and over the cuticular surfaces. Such an increase in vapor pressure within would usually be adjusted *pari passu* with the rise in temperature, by the ejection of an increasing amount of water vapor through the stomatal openings, and if the temperature were to remain constant for a time the rate of water loss during such a period would be somewhat greater than at the lower temperature, the slightly greater rate being due to the more rapid vaporization and diffusion at higher temperatures.

But the rise in temperature of air and of leaf are not our main consideration with reference to openly exposed green foliage upon a sunny day. Air and leaf do continuously increase in temperature from early morning till some time in the afternoon, but in the meantime the radiant energy of the sunshine is ever being absorbed to a greater or less extent by the green leaf tissue, so that this tissue should tend to become warmer than the air. By far the larger portion of this absorbed energy (a negligible portion disappears through photosynthetic changes) must operate to increase the vapor tension of the water films which surround the foliar air spaces or are held in the epidermal walls. Evaporation from these films must thus be increased, the latter remaining nearly constant in temperature. The accelerated evaporation within the leaf should produce in its turn an increase in the partial gas pressure due to water vapor in the internal atmosphere, and hence, the

stomata being open, a more rapid diffusion, or possibly a molar movement,[4] of water vapor through these openings into the outer air. As long as the sun shines, then, a high rate of transpiration may be maintained, and this without excessively high temperatures in the foliar tissues. The radio-atmometer (LIVINGSTON, see footnote 3) furnishes an excellent example of this kind of effect; with continuous influx of solar energy evaporation from the black porous cup is maintained at a high rate, but the black cup does not exhibit any markedly higher temperature than does the white one, from which water loss is much less rapid.

The Piche atmometer[5] illustrates this process, and also shows another phenomenon which we need to consider here. It consists of a graduated glass tube, closed above and covered below with a circle of filter paper, the latter having a pin hole to admit air to the tube. The tube is filled with water, the paper disk applied and fixed in place, and the whole inverted. The entire disk soon becomes wet, and evaporation therefrom draws water from the tube, air rising through the pin hole to replace the water withdrawn. Now, if such an instrument be arranged with a relatively large disk of paper and placed in conditions of pronounced evaporation, it may often be noted (we are unable to find any mention of this in the literature) that the outer edge of the disk becomes dry, thus vitiating the readings as a measure of the evaporating power of the air. The instrument is unsuited to its purpose unless care be exercised to have the paper so small that the evaporation rate never surpasses the possible rate of outward diffusion to the periphery of the disk. As long as the peripheral portion of the paper remains unsaturated, the actual rate of water loss is maintained nearly constant, the dry area automatically increasing or decreasing in extent according to the fluctuations in the amount of energy

[4] According to the researches and calculations of BROWN and ESCOMBE (Static diffusion of gases, etc., in plants. Phil. Trans. Roy. Soc. London 193:223–291. 1900), no molar or streaming movement needs to be postulated to explain the highest rates of transpiration observed by these authors in southern Britain. Whether a molar streaming may not occur about midday in the Arizona desert remains an open question.

[5] For literature bearing on this instrument, see LIVINGSTON, GRACE J., An annotated bibliography of evaporation, reprinted from Monthly Weather Review, 1908–1909. The original description is abstracted at page 48 of the reprint under "1872, Piche."

absorbed. Thus, an increase in the evaporating power of the air or in the intensity of impinging solar energy may, with such an instrument, bring about an actual decrease in the extent of the evaporating surface and hence a retardation of water loss. While the actual rate of water loss remains constant so long as the paper is not completely wet, the *relative* rate of water loss (as the loss from the instrument might be compared with that from an open pan of water similarly exposed) begins to decrease as soon as the peripheral portion of the paper begins to dry out. Of course the drying of the disk and the accompanying retardation of relative evaporation are due to a fall below unity of the ratio of possible water supply to water loss; since the rate of possible supply in this instrument remains constant, this means an increase in the denominator of the ratio. A similar result might be occasioned if the rate of loss were to remain constant and the rate of possible supply were to be decreased.

This sort of inadequacy in the rate of water supply to maintain the original evaporating surface during periods of high evaporation may be postulated as perhaps the main feature in bringing about the somewhat sudden fall in relative transpiration observed in the early portion of the day. Indeed, a Piche atmometer may be so arranged, with an abnormally large, preferably *blackened*, disk, so that if compared to a pan of water or to a porous cup atmometer it will exhibit a graph of *relative evaporation* for the daylight hours quite closely paralleling the corresponding graph of relative transpiration for a green plant similarly exposed.

It is only logically conceivable that there exists, for each leaf at any particular time, a maximum possible rate of inward movement of water through the petiole, and if the rate of water loss at any time surpass this possible rate of supply, the tissues of the leaf should become less moist, following the analogy of the Piche atmometer described above. This supposed process of drying out of the foliar cell walls which abut upon the internal atmosphere has been termed *incipient wilting*[6] by the author last cited. It should take place

[6] Since an *incipient* process must be regarded as already actually occurring, it is quite illogical to apply the term *wilting* to a condition of affairs which by definition is not accompanied by any wilting at all. We have therefore adopted the term *incipient drying* in place of the other term.

rapidly at first and more slowly later, the water films gradually retreating into the pores of the cellulose and not only decreasing the extent of the exposed evaporating surfaces, but also greatly increasing the surface tension of the latter. When the surface tension of a liquid film is increased, its vapor tension is correspondingly decreased,[7] so that incipient drying of these exposed cell walls should be accompanied by a marked fall in the rate of vaporization of water therefrom. This should mean nothing less than a measurable retardation in the relative rate of water loss, a retardation *due to an excessive evaporation rate*.[8]

A physical parallel of this phenomenon may readily be arranged by mounting one of two similar paper disks as in the Piche atmometer, so that it will be constantly supplied with water, and its water content will remain constant during the progress of evaporation, while the second disk is similarly mounted on an empty tube, so that its moisture content will fall with water loss. An experiment of this sort, carried out by weighings in the laboratory, showed that a fall in the moisture content of the paper of 6 per cent produced a corresponding decrease in the rate of evaporation of 5 per cent. Similarly, a fall of 17 per cent in water content was accompanied by an evaporation rate 8 per cent lower than when the paper was saturated. The effect becomes more and more pronounced as the paper dries out; when only 54 per cent of the original moisture was present the rate of water loss had diminished to 77 per cent of that from the saturated disk.

[7] PATTEN, H. E., On the relation of surface action to electrochemistry. Trans. Am. Electrochem. Soc. **19**:359–380. 1911. Also, FREUNDLICH, H., Kapillarchemie. Leipzig. 1909. p. 46.

DIXON has presented the only experimental evidence of this with which we are acquainted. DIXON, H. H., Transpiration and the ascent of sap. Prog. Rei. Bot. **3**:1–66. 1909. p. 51.

[8] RENNER has pointed out this same thing: "Denn wenn die Wasserzufuhr ausbleibt, müssen die Membranen trockener werden und damit die Transpiration weiter sinken. . . . ." RENNER, O., Beiträge zur Physik der Transpiration. Flora **100**: 451–547. 1910. p. 516; see also p. 520.

The same author has contributed a most excellent analysis of the water relations of stem and leaf, many points of which have a bearing upon the present question, but we are unable to do more here than merely to mention the paper: RENNER, O., Experimentelle Beiträge zur Kenntnis der Wasserbewegung. Flora **103**:171–247. 1911.

If the cellulose membranes which are adjacent to the air spaces of the leaf and those bathed by the outer air were structurally similar to the filter paper used in the test just described, the above figures might be applied to the moist foliar surfaces. But we may be sure that filter paper possesses a much less compact structure than any cell membrane in the plant; hence, the reduction in the evaporation rate brought about by partial drying out of the moist cell walls should be much more marked in the case of the latter than is manifest in our experiment. It seems quite probable that a reduction of 50 per cent in the water content of exposed cellulose walls should produce an equal or much greater reduction in the evaporation rate therefrom, and in the case of cutinized epidermis (which holds but little moisture when saturated, and from which cuticular transpiration takes place), the effect of partial drying out should be still greater.

It appears, therefore, quite within the limits of possibility, that the phenomenon of incipient drying of exposed membranes (internal and external) may be adequate to cause the non-stomatal hindrance to transpiration here considered. It should make no difference whether the excessive rate of water loss from foliage leaves be brought about by high evaporating power of the air, by absorption of sunshine, by continually rising temperature, or (merely relatively) by a decrease in the possible rate of water supply (as by the drying of the soil or by the removal or injury of the basal part of the plant), the effect must be the same in every case, namely, a marked fall in the rate of relative transpiration.

If such a process of drying out in leaf tissue were continued, water would eventually be extracted from the protoplasmic membranes, which would in turn remove moisture from the vacuoles, and (since we suppose that the rate of supply from the vascular elements to be inadequate) the turgor pressure would decrease. Finally, all internal pressure would be removed from the cell walls, which would thus cease to be under strain, and all turgidity would thus be destroyed; the wilting point would be reached. Continued still further, the process would result in actual plasmolysis of the cells and finally in death, after which desiccation would rapidly take place. The latter portion of this supposition seems

applicable in all cases when leaves wilt and dry through the influence of too great an intensity of transpiration or too low a maximum possible rate of water supply, these two causes being merely different aspects of the same condition, namely, that the ratio of supply to demand is less than unity.

(2) Other possible factors in the production of an internal resistance to water loss

Logically, there are other possible causes for the observed fall in relative transpiration; it might be regarded as brought about by increased concentration either of the extracellular liquid (in and upon the cell walls), or of the cell sap within the cell vacuoles (as by photosynthesis), or by decreased permeability (perhaps some sort of hardening or coagulation) of the protoplasmic layer itself. The recent work of Fitting[9] shows that the osmotic pressures in the vacuoles of the foliage of desert plants in moist soil (these conditions agree with those of Livingston's plants) are usually isosmotic with a solution less concentrated than 2-molecular potassium nitrate. The fact that no wilting was apparent in the Arizona experiments upon which we are basing our work (which means that turgidity was maintained) indicates clearly that the concentration of the cell sap must have been *higher* than that of the extracellular solutions. Thus the maximum concentration of the evaporating solutions which can be postulated is surely no greater than that of a 2-molecular solution of potassium nitrate, and in order to be certain that our error is in the right direction, we may assume maximum concentrations isosmotic with a 3-molecular solution of this salt. The minimum concentration (as in the early morning) can never be zero, but we once more take this as an assumed limit far beyond the actual, and ask the question, if the foliar solutions vary from pure water to a concentration isosmotic with 3-molecular potassium nitrate, what may be the relative magnitude of the resulting retardation of evaporation? Other conditions being equal, evaporation is known to be proportional to the vapor tension of

[9] Fitting, Hans, Die Wasserversorgung und die osmotischen Druckverhältnisse der Wüstenpflanzen. Zeitschr. Bot. 3:209–275. 1911. See also Livingston, B. E., The relation of the osmotic pressure of the cell sap in plants to arid habitats. Plant World 14:153–164. 1911.

the evaporating surface, and the vapor tension (and hence the evaporation) of a 3-molecular solution of potassium nitrate is only about 8 per cent lower than that of pure water. A comparison of this figure with 49 per cent, the approximated retardation in transpiration, leads us to conclude that an increased concentration and the accompanying lowerings of vapor tension of the foliar solutions cannot possibly be directly related to the great fall in relative transpiration which is observed.[10] That such variations in concentration may have some indirect effect is highly improbable, and there is no evidence at hand to enable us to consider this possibility here. That a slight diurnal increase in the concentration of solutions bathing the protoplasmic membranes might bring about marked changes in the colloidal state of the latter, and hence in their permeability to water, is of course possible; but if such were the case, the effect would be manifest simply as a lowering of the possible rate of supply to the cell walls, resulting in a partial drying out of these, so that the phenomenon would appear as incipient drying.

We conclude, therefore, that the hypothesis of incipient drying, due to partial drying of exposed membranes, is the only adequately possible explanation of the diurnal fall in relative transpiration. If this process actually occurs, it should be exhibited in a sensible decrease in the actual moisture content of the leaves concerned. We should thus expect to find the moisture content of sun-illuminated foliage to become less as the day advances, attaining a minimum some time in the afternoon and then rising again. Whether or not this is actually manifest, as a diurnal fall in the percentage of foliar moisture, is the question which we have experimentally attacked.

It needs to be added here that the hypothesis of incipient drying, while apparently the only logically possible explanation of the non-stomatal *hindrance to water loss*, is not the only logically possible cause of a marked diurnal *fall in the relative water content of* green leaves. With the actual water content of the tissues remain-

[10] This conclusion is quite in accord with that reached by DRABBLE and DRABBLE. See DRABBLE, E., and DRABBLE, H., The relation between the osmotic strength of cell sap in plants and their physical environment. Biochem. Jour. 2:117–132. 1907.

ing constant, a diurnal accumulation of non-aqueous materials, as of carbohydrates, oils, proteins, etc., might result in a great increase in the contained non-aqueous material, and a corresponding fall in the percentage of moisture. Such an accumulation, with its accompanying decrease in the percentage of moisture, however, would have no marked influence upon relative transpiration. This question may be studied quantitatively through the daily fluctuations in relative water content on the basis of unit leaf area, a phase of the problem with which we have not concerned ourselves.

Experimentation

Our method of experimentally attacking the problem as to whether a definite diurnal fall in the percentage of leaf moisture actually occurs was to gather, at different hours of the day and night, a large number of similar leaves from plants growing in the open soil, and to determine the percentage of moisture therein contained by the common method of weighing, drying at 100° to 105° C., and reweighing. As the leaves were gathered they were placed immediately in tarred glass bottles and tightly stoppered. After being weighed, the open bottles were placed in the drying oven, and the final dry weight obtained without removing or handling the leaves. A large number of plants were available for this work, so that but few leaves were taken from the same plant, and the numerical result may be taken as fairly well approximating the average condition of the whole plot of plants of the species tested. The plants used were all spontaneous in the open ground near the Desert Laboratory. In some cases the sample leaves were taken every two hours, in others less often, and a porous cup atmometer was operated and read at short intervals in the vicinity of the group of plants from which leaves were taken. The work was carried out at the Desert Laboratory of the Carnegie Institution at Tucson, Arizona, in the summer of 1910.

Preliminary tests of the leaf moisture in *Physalis angulata* var. *Linkiana* Gray and in *Martynia louisiana* Mill., made on July 28, showed that the moisture content of the *Physalis* leaves was 744.7 per cent of the dry weight at 6 A.M., and only 561.0 per cent at 2 P.M., while the corresponding percentages in *Martynia* leaves were

543.3 and 377.3 per cent, respectively. Expressed in another way, the non-aqueous materials of the leaves made up for *Physalis* 12 per cent of the whole in the morning and 15 per cent in the afternoon, while for *Martynia* these quantities were 16 and 21 per cent, respectively. It thus became clear that there had occurred a marked fall in the relative moisture content of these leaves during the period from 6 A.M. to 2 P.M., which is what our a-priori considerations had led us to expect, and our problem seemed to be answered in the affirmative.

We present, in the four following tables, the data derived from a number of other tests, carried out by a method quite similar to that followed in the two tests just described. Besides the two plants named above, we dealt with *Nicotiana glauca* Graham (a woody perennial attaining the proportions of a tree), *Euphorbia heterophylla* L., *Trianthema Portulacastrum* L. (a fleshy plant resembling *Portulaca oleracea* L. of the east), *Tribulus terrestris* L., *Sida angustifolia* Lam., *Amarantus Palmeri* Wats., *Maclura pomifera* (Raf.) Schneider, *Covillea glutinosa*, and *Prosopis velutina* Wooton. The two last-named plants are characterized by thin, hard, xerophyllous leaves, the foliage of *Covillea* (the creosote bush) being heavily covered with a shellac-like resinous layer. For the naming of our experimental plants we are indebted to the kindness of Professor J. J. THORNBER, of the University of Arizona.

Tables I to IV present the evaporation rates for the periods in question, in terms of cc. from the standard porous cup atmometer.[11] The moisture contents of the leaves are given in percentages of their dry weight, also the dry weights in percentages of total weight. In the first two columns appear periods and evaporation rates per hour (cc.) from the porous cup atmometer, these data being quite comparable throughout all four series. Evaporation maxima are designated by asterisks. In the third column are presented the hour at which leaf tests were made. The remainder of each table presents the leaf moisture data, each minimum being denoted by an asterisk in the second column for each plant, and all the maxima by full-faced type.

[11] LIVINGSTON, B. E., Operation of the porous cup atmometer. Plant World 13:111–118. 1910.

It is at once apparent that in all cases but three (nine out of eleven species) our question (page 319) has been answered very definitely in the affirmative.[12] In the case of *Prosopis* (table III) the minimum water content, at midday, is only slightly below that in

TABLE I

AUGUST 12–13, 1910

EVAPORATION		PERCENTAGE OF MOISTURE						
			Martynia		Sida		Amarantus	
Period	cc. per hr.	Hour of test	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight
(A.M.)								
6– 7	0.66	6	417.6	81	452.8	82	539.4	84
7– 8	1.14	7	390.0	80	484.3	83	533.3	84
8– 9	2.28	8	394.6	80	412.5	80	551.2	85
9–10	2.34	10	384.2	79	353.7	78	500.7	83
10–11	2.58	..	.....	..	.....	..	.....	..
11–12	2.52	12	357.6	78	355.7	78	490.6	83
(P.M.)								
12– 1	3.48	..	.....	..	.....	..	.....	..
1– 2	3.90	2	339.3	77	338.9	77	395.0	80
2– 3	3.54	..	.....	..	.....	..	.....	..
3– 4	3.72	4	338.4	77*	307.3	75*	379.6	79
4– 5	4.02*	..	.....	..	.....	..	.....	..
5– 6	2.52	6	371.2	79	317.1	76	366.6	79*
6– 7	1.56	..	.....	..	.....	..	.....	..
7– 8	1.44	8	551.6	85	407.2	80	591.5	86
8– 9	1.32	..	.....	..	.....	..	.....	..
9–10	1.08	10	502.7	83	444.4	82	539.2	84
10–12	0.69	12	461.5	82	457.1	82	601.9	86
(A.M.)								
12– 4	0.125	4	494.7	83	457.0	82	530.0	84
4– 5	0.72	..	.....	..	.....	..	.....	..
5– 6	0.60	6	455.1	82	.....	..	542.1	84

the early morning, and the maximum, at 4 P.M., is not markedly above the minimum; this case is questionable. One of the two definite exceptions to the general rule, *Covillea* (table III), appears to exhibit a reversal of the usual variation in water content. The fact that this plant and *Prosopis* are non-succulent xerophytes is

[12] At about the same time that our experiments were in progress, LLOYD carried out his recently published tests in regard to this same matter in *Fouquieria*. He finds and discusses a diurnal fall in the relative water content of the foliage of this plant. LLOYD, F. E., The relation of transpiration and stomatal movements to the water content of the leaves in *Fouquieria splendens*. Plant World 15:1–14. 1912.

possibly to be correlated with their peculiar behavior, and it may be suggested that such permanent structural retardation of water loss as is present in the foliage of such types may have to do with preventing a marked decline in leaf moisture by day. Such plants seem worthy of further study in this connection. The other excep-

TABLE II

AUGUST 21–22, 1910

EVAPORATION			PERCENTAGE OF MOISTURE									
			Physalis		Nicotiana		Euphorbia		Trianthema		Tribulus	
Period	cc. per hr.	Hour of test	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight
(A.M.)												
4– 5	0.06	5	......	..	**588.7**	**85**	......	..	......	..	**435.6**	**81**
5– 6	0.06	..	......	..	......	..	......	..	......	..	......	..
6– 7	0.50	7	820.2	89	......	..	**581.6**	**85**	**1203.9**	**92**	......	..
7– 8	1.20	..	......	..	......	..	......	..	......	..	......	..
8– 9	1.92	9	865.5	90	435.0	81	521.6	84	1197.9	92	352.5	78*
9–10	2.10	10	804.6	89	......	..	......	..	......	..	......	..
10–11	2.40	11	818.9	88	......	..	......	..	......	..	......	..
11–12	2.58	..	......	..	......	..	......	..	......	..	......	..
(P.M.)												
12– 1	2.40	1	678.5	87	423.3	81	433.8	81*	758.0	89*	378.8	79
1– 2	2.88	..	......	..	......	..	......	..	......	..	......	..
2– 3	2.94*	3	660.6	87*	......	..	......	..	......	..	......	..
3– 4	2.70	..	......	..	......	..	......	..	......	..	......	..
4– 5	2.70	5	703.4	87	392.5	80*	485.5	83	825.2	89	420.1	81
5– 6	1.92	..	......	..	......	..	......	..	......	..	......	..
6– 7	1.20	7	**877.9**	**90**	......	..	......	..	......	..	......	..
7– 8	1.20	..	......	..	......	..	......	..	......	..	......	..
8– 9	1.20	9	855.7	90	......	..	480.9	83	......	..	430.6	81
9–10	0.90	..	......	..	......	..	......	..	......	..	......	..
10–11	1.98	..	......	..	......	..	......	..	......	..	......	..
11–12	1.14	..	......	..	......	..	......	..	......	..	......	..
(A.M.)												
12– 1	0.42	..	......	..	......	..	......	..	......	..	......	..
1– 2	0.42	..	......	..	......	..	......	..	......	..	......	..
2– 3	0.18	3	848.2	89	......	..	......	..	......	..	......	..

tion to the usual behavior is that of *Physalis* (table IV). For this species we have two cases exhibiting the usual behavior (besides the preliminary test, which makes three), and it is noted that the exceptional case occurs on a day with very low evaporation.

Table V presents a summary of the data of the preceding tables. The minimum and maximum water content and the hours at which

these occurred, the latter being simply numbered from 1 to 24, are there given, together with the corresponding maximum rate of evaporation and the hour of its occurrence.

TABLE III

AUGUST 28–29, 1910

Evaporation		Percentage of moisture								
			Physalis		Maclura		Covillea		Prosopis	
Period	cc. per hr.	Hour of test	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight	On basis of dry substance	On basis of entire weight
(A.M.)										
6–7	0.82	7	778.5	89	**237.2**	**70**	116.7	54*	159.7	61
7–8	2.37	..	.....	..	.....	..	.....	..	.....	..
8–9	2.87	9	736.7	88	224.1	69	127.4	56	145.3	59
9–10	3.77	..	.....	..	.....	..	.....	..	.....	..
10–11	4.51	11	595.2	86	.....	..	.....	..	.....	..
11–12	4.92	..	.....	..	.....	..	.....	..	.....	..
(P.M.)										
12–1	5.08*	1	566.2	85*	186.6	65	125.1	56	144.3	59*
1–2	4.67	..	.....	..	.....	..	.....	..	.....	..
2–3	3.03	3	625.9	86	173.8	63*	.....	..	.....	..
3–4	3.69	4	.....	..	.....	..	**139.3**	**58**	**168.4**	**61**
4–5	2.13	5	780.6	89	.....	..	.....	..	.....	..
5–6	1.56	..	.....	..	.....	..	.....	..	.....	..
6–7	1.15	7	**781.1**	**89**	.....	..	.....	..	.....	..
7–8	1.56	..	.....	..	.....	..	.....	..	.....	..
8–9	0.90	9	772.1	89	186.9	65	.....	..	.....	..
9–10	0.90	..	.....	..	.....	..	.....	..	.....	..
10–11	0.57	11	761.5	88	.....	..	.....	..	.....	..
11–12	0.49	..	.....	..	.....	..	.....	..	.....	..
(A.M.)										
12–1	0.74	1	696.1	87	.....	..	.....	..	.....	..
1–2	0.33	..	.....	..	.....	..	.....	..	.....	..
2–3	0.41	3	705.4	88	.....	..	.....	..	.....	..
3–4	0.33	..	.....	..	.....	..	.....	..	.....	..
4–5	0.33	5	743.4	88	.....	..	.....	..	.....	..
5–6	0.82	..	.....	..	.....	..	.....	..	.....	..
6–7	1.48	7	755.2	88	.....	..	.....	..	.....	..

Physalis is the only form which was tested on different days, with different conditions of evaporation, and the data therefrom are the most instructive of our series. In the first two cases this form showed the greater variation in water content with the higher evaporation maximum (5.08 cc. per hour, table III), and the smaller variation with the lower evaporation maximum

(2.94 cc. per hour, table II). In the third test the water variation was slightly (probably within the limits of experimental error) in the opposite direction, as has been noted. The evaporation maximum on this day was relatively low, 2.52 cc per hour (table IV). These relations make it appear that the amount of variation in foliar moisture is directly related to the evaporating power of the air, especially to the maximum intensity of this factor for the day

TABLE IV

AUGUST 30, 1910

Evaporation		Percentage of moisture		
			Physalis angulata	
Period	cc. per hour	Hour of test	On basis of dry substance	On basis of entire weight
(A.M.)				
7- 8	1.97	7	668.2	87
8- 9	1.56	9	695.0	87
9-10	1.72	..	.....	..
10-11	2.46	11	680.7	87
11-12	2.30	..	.....	..
(P.M.)				
12- 1	2.30	1	714.7	88
1- 2	2.52*	..	.....	..
2- 3	2.30	3	662.3	87*
3- 4	2.30	..	.....	..
....	....	..	.....	..
4:30-5:30	0.97	5:30	665.7	87

NOTE.—The day was almost wholly cloudy, which accounts for the generally low evaporation rates and the small fluctuations.

in question. With great evaporation there appears to be a great diurnal fall in moisture content, with less evaporation a less pronounced fall, and with still less evaporation no fall at all, possibly even a slight rise.

Only a single test, with measurement of evaporation, was carried out with each of the remaining forms. The greatest variations were exhibited by *Martynia*, *Amarantus*, and *Sida*, all of them being plants which have been repeatedly observed to wilt very readily under drought conditions. The only true succulent tested was *Trianthema*, which showed a variation markedly greater than that of *Physalis* for the same day (table II). *Nicotiana* and

Euphorbia gave variations equaling *Physalis* (tables II and III); those of *Tribulus* and *Maclura* were markedly less; while, as already noted, *Prosopis* and *Covillea* evidence very small variations, that of the latter rather definitely in the opposite direction.

Scrutiny of table V brings out the fact that the hours of minimum relative water content for the prevailing type of leaves falls generally within an hour or two of that of the maximum evaporation rate. The minimum moisture content occurs between 1:00 P.M. and 5:00 P.M. for all cases except those already noted as exceptional, and that of *Tribulus* (table II), which has its minimum at 9:00 A.M.

TABLE V

SUMMARY OF TABLES I–IV

Plant	Minimum moisture content		Maximum moisture content		Maximum of evaporation	
	Percentage	Hour	Percentage	Hour	cc.	Hour
Martynia (table I)	77	14	85	20	4.02	16–17
Sida (table I)	75	16	83	7	4.02	16–17
Amarantus (table I)	79	16, 18	86	20, 24	4.02	16–17
Physalis (1) (table II)	87	13, 16	90	19, 21	2.94	14–15
Physalis (2) (table III)	85	13	89	17, 19, 21	5.08	12–13
Physalis (3) (table IV)	87	15, 17½	88	13	2.52	13–14
Nicotiana (table II)	80	17	85	5	2.94	14–15
Euphorbia (table II)	81	13	85	7	2.94	14–15
Trianthema (table II)	89	13, 17	92	7, 9	2.94	14–15
Tribulus (table II)	78	9	81	5, 17, 21	2.94	14–15
Maclura (table III)	63	15	70	7	5.08	12–13
Covillea (table III)	54	7	58	16	5.08	12–13
Prosopis (table III)	59	9, 13	61	7, 16	5.08	12–13

The evidence from *Physalis*, indicating clearly a definite relation between the magnitude of the moisture variation and the intensity of evaporation, may be interpreted to mean that the variation is due primarily to incipient drying (to a removal of water by transpiration more rapidly than its entrance into the leaves), and not to an accumulation of non-aqueous bodies in the leaf cells. It seems extremely improbable that a diurnal accumulation of plastic materials should exhibit such a parallelism with the evaporation

as do our data of moisture variation, from which consideration it may be concluded that the variation is probably not causally related to such accumulation of substances. While there are several observations in the literature which bear more or less directly upon this matter of the diurnal accumulation of soluble and insoluble bodies in the leaf, we do not as yet possess data adequate to a logical discussion. This should be made the subject of a special study in the present connection.

Following the criterion of the *time of occurrence* of the minimum water content (2 to 5 P.M.) and of that of the maximum in relative transpiration, as brought out in Publ. 50, Carnegie Inst. (10 A.M. to 1 P.M.), it appears highly probable that there exists a causal relation between these two phenomena. Since the critical point in the graph of relative transpiration denotes, as has been pointed out, the entrance into operation of some internal check or hindrance to the loss of water vapor, and since a decrease in relative water content should be effective to produce such a check long before the water content had attained its minimum, we should expect the maximum in relative transpiration to occur long before the hour of least foliar moisture, which it appears actually to do. We may conclude tentatively, and on general lines, that, for the ordinary types of leaves, the retardation in water loss is manifest several hours before the time of minimum water content. After the critical point in relative transpiration, the non-stomatal retardation of water loss appears to be (Publ. 50) continuously active until well into the night, its effects becoming mingled with those of stomatal closure at or about sunset. It appears to be gradually removed during evening and early night, so that in the hours just preceding sunrise stomatal retardation seems to be alone manifest. If the non-stomatal effect be due to decreased water content, it should be removed when the leaves had regained their normal moisture, which condition is quite met by the observations. The maximum in moisture content (except in the few erratic cases already mentioned) occurs in the night or early morning, just as our hypothesis demands.

The only direct comparison between the daily march of leaf moisture and that of relative transpiration which has been made

thus far, was carried out on August 21 and 22. From 5 A.M. on the first day till 6 A.M. on the second, hourly weighings were made on two potted and sealed plants of *Physalis*, while corresponding readings were obtained from a porous cup atmometer having the same exposure. The two plants were similar to each other and, though somewhat smaller, not dissimilar to the *Physalis* plants of the leaf moisture tests of the same period (table II), so that the two series of data are fairly comparable. Space will not permit the presentation here of the transpiration and evaporation rates and of the resulting ratios and graphs, but we may mention the findings of most present interest. Averaging the data for the two plants (these data are very similar), the maximum of absolute transpiration occurred from 11 A.M. to 12 noon, while the maximum rate of loss from the porous cup atmometer fell three hours later. The maximum of relative transpiration occurred from 12 noon to 1 P.M.; thus the non-stomatal retardation of water loss became effective about 1 P.M. As already shown (table II), the moisture content of the leaves of *Physalis* in the open soil fell during the period from 9 A.M to 3 P.M., and rose again to its maximum, or what we may term its normal, at 7 P.M. From these data we see that the non-stomatal retardation of water loss became manifest in the potted plants four hours after the leaf moisture had begun to decrease in the plants in the open, and two hours before the occurrence of the minimum water content. The maximum evaporation rate occurred in the hour preceding the minimum water content. All of these points are quite in harmony with the requirements of the hypothesis of incipient drying, and the data appear to substantiate this hypothesis, so far as their incomplete nature will allow.

The work of BRIGGS and SHANTZ[13] on some of the conditions which determine wilting has thrown not a little indirect light upon the question of the occurrence of incipient drying. By the ingenious balanced system which these authors devised, they have shown clearly that, with the gradual drying out of the soil, there comes a time when the rate of entrance of water into the upper part of a plant is surpassed by the transpiration rate. This is, of course,

[13] BRIGGS, L. J., and SHANTZ, H. L., The wilting coefficient for different plants and its indirect determination. Bur. Pl. Ind. Bull. 230. 1912.

the condition of incipient drying. Judging from the rates of transpiration shown by the tables of this contribution (no attempt is made to define the aerial conditions), it appears that the evaporating power of the air during the experiments there described was relatively low. This fact rendered the process of incipient drying, which leads eventually to actual wilting, very much prolonged, and it is perhaps not surprising that these authors failed to detect incipient drying in the plants which actually wilted, making the mistake of supposing that incipient drying in the non-wilting forms (as cactus, lemon, etc.) is to be considered as identical with actual wilting (which is relatively a much later occurrence) of ordinary thin-leaved plants. It is greatly to be regretted that such an expensive and elaborate series of determinations as BRIGGS and SHANTZ have made should have been carried out without records of the intensity and duration aspects of the evaporating power of the air under which the experiments were performed. Such records, which are perhaps the most readily obtained of all the climatic records which are as yet available for the study of plant processes, would have made possible the duplication of the aerial conditions of these experiments and would have aided greatly in the further analysis of some of the important findings of these authors.

Conclusions

We conclude from our measurements and comparisons that there can remain little question that green plants when subjected to relatively great diurnal evaporation intensity, at least frequently exhibit a marked fall in foliar moisture content by day and a corresponding rise by night. The daily march of evaporation remains still to be studied in other climates than that of summer in southern Arizona, so that we are unable to compare our conditions with those of more humid or cooler regions. From our experience with cloudy weather, we are inclined to the prediction that the diurnal decrease in leaf moisture here established for high evaporation rates may fail to occur in regions of low evaporation when accompanied by relatively high rates of soil moisture supply.

Our studies also indicate that some non-succulent, small-leaved xerophytes (such as *Covillea* and *Prosopis*) fail more or less com-

pletely to exhibit a diurnal fall in foliar moisture under conditions of evaporation which render it manifest in the common type of thin-leaved plants (such as *Martynia*, *Sida*, *Physalis*), as well as in such pronounced succulents as the *Portulaca*-like *Trianthemum* of our work. It is suggested that these exceptional small-leaved xerophytes may actually show a somewhat higher leaf moisture content by day than by night, but this proposition is uncertain.

While the other logically possible cause of this diurnal decrease in relative water content of foliage leaves, namely, a diurnal increase in materials other than water within the tissues, remains still to be considered in a thoroughly adequate way, our findings fail to adduce evidence in favor of this as the true cause of the observed phenomena, and do furnish several lines of indirect opposing evidence. It may be stated, therefore, that, so far as evidence is at hand (including indirect considerations of the literature, not here cited), it is probable that the cause of this diurnal minimum in foliar moisture rests in the phenomenon of incipient drying, brought about whenever the ratio of water loss to water supply in the leaves is rendered less than unity. It may thus be suggested that, although our tests with *Physalis* would lead to the conclusion that the external factor which controls this diurnal fall of leaf moisture is evaporation intensity simply, the true controlling condition is more probably the ratio of water supply to water loss. Thus, the structure of the plant (including all of its various "adaptations" to dry habitats), the moisture conditions of the soil, intensity of evaporation and of solar illumination appear to make up the controlling environmental complex.

It seems highly probable from our studies that the diurnal, non-stomatal retardation of the escape of water vapor from green leaves in sunlight (as first described in Publ. 50, Carnegie Inst., and there attributed to the influence of temperature or evaporation intensity) is but the effect of a lower vapor tension within the internal atmosphere of the leaves and over their surfaces, this lower vapor tension being brought about by the increased surface tension and decreased evaporating surface which accompanies a lowered water content of the internally and externally exposed cell walls.

In conclusion, it may be suggested that we have here, in the

diurnal minimum in the water content of foliage leaves, a criterion that may be of some importance to scientific agriculture, at least in the arid regions of the globe. By this criterion it may be possible to determine indirectly, and somewhat simply, the status of the water relations of the plant, and indeed to foresee the need of increased soil moisture, long before the usual criterion of cessation of growth or actual wilting becomes manifest.

THE JOHNS HOPKINS UNIVERSITY
BALTIMORE, MD.

BUREAU OF SCIENCE
MANILA, P.I.

RAY TRACHEIDS IN ABIES

W. P. THOMPSON

(WITH PLATES XXIV AND XXV)

A characteristic feature of the Abietineae, as opposed to the remaining tribes of the Coniferales, is the possession of ray tracheids in their wood. To this statement exception must be made, on the one hand for the genera *Abies* and *Pseudolarix*, from which they have hitherto been regarded as quite absent, and on the other hand for a few species of the Taxodineae and Cupressineae, in which they have been reported to occur sporadically. Even in the latter, however, they never become normal features as in the Abietineae. This distribution has recently received two interpretations. PENHALLOW[1] held that in the species where they occur sporadically they are appearing for the first time, and from this condition develop to their culmination in the Abietineae. JEFFREY,[2] on the other hand, having observed their occurrence in association with a wound in *Cunninghamia sinensis*, regards their sporadic appearance as a reminiscence of an original abundant condition such as exists in the Abietineae. The application of these conflicting views in phylogenetic considerations of the whole family is obvious.

To the distribution briefly outlined above, the writer[3] recently recorded an exception in the case of the genus *Abies*. In a wounded root of *A. amabilis* ray tracheids were discovered in considerable numbers. The only other record of their occurrence in the genus was made by PENHALLOW (*loc. cit.*), who observed them sporadically in *A. balsamea*. In view of the peculiar circumstances of their discovery and its bearing on the theories in vogue, it was considered advisable to investigate the material of *A. amabilis* fully and to examine other species of the genus.

The material in which the marginal tracheids were observed

[1] PENHALLOW, D. P., North American Gymnosperms. Boston. 1907.

[2] JEFFREY, E. C., Traumatic ray tracheids in *Cunninghamia sinensis*. Ann. Botany 22:602. *pl. 31*. 1908.

[3] THOMPSON, W. P., The origin of the ray tracheids in the Coniferae. BOT. GAZ. 50:101–116. 1910.

consisted of a segment of a root several inches in length and containing about 25 annual rings. On one side a severe wound had been partially healed over. A photograph of a transverse section taken some distance above the wound is presented in fig. 1. Even at this low magnification, characteristic tangential series of traumatic resin canals may be observed in the 5th, 6th, 9th, and 12th annual rings. Therefore, the root must have been wounded at least four times. The repeated wounding had apparently sapped its vitality, for the later-formed annual rings were very narrow and infested with fungus filaments.

A more magnified view of one of the series of canals is shown in fig. 2. The arrangement is seen to be typically traumatic. In other respects the wood is of the normal *Abies* type.

A radial longitudinal section, taken at some distance from the outermost wound, is photographed at rather low magnification in fig. 3. Near the left of the figure the septated element and its neighbor on the right, which is also septated beyond the limits of the figure, form part of the traumatic series between the canals. Immediately on their right two ray tracheids are to be seen on the upper margin of the ray. The magnification is not sufficient to show the character of their pits except that they are smaller than those of neighboring wood tracheids.

The character of the pits on a similar element may be distinguished, however, in fig. 4, which is a photograph at a higher magnification of another section. Two of the pits in section on the extreme left are clearly bordered on the upper side and simple on the parenchyma side. The others, though not so clear, are likewise unilaterally bordered; therefore the long low element is a ray tracheid.

That interspersed as well as marginal tracheids are present is shown in fig. 5. The two pits on the conspicuous vertical end wall are distinctly bordered, as are those on the horizontal walls of the same cells. Therefore, these cells are ray tracheids occurring between the parenchymatous cells of the ray which are to be seen above and below. The parenchymatous cell below the ray tracheid is traversed by a filament of the fungus which probably gained entrance at the wounds.

Elongated ray tracheids of the type described by the writer (*loc. cit.*) as common in the young root of *Pinus* were also frequently observed. One of them is shown in fig. 9. The tail-like projection extends to the extreme upper right of the figure. A unilateral bordered pit may be observed in contact with the ray and a bilateral one in contact with a wood tracheid.

The figures just described show that ray tracheids of all kinds are present in this wounded root of *A. amabilis*. Normal material of the same species, root, stem, and branch was carefully examined, and, in accordance with all former observations, not a single ray tracheid found. Therefore, it must be concluded that those observed were in definite association with the wounds. In fact, their occurrence recalls precisely that described by JEFFREY for *C. sinensis*. Occurring, as they do, in one of the two abietineous genera which normally are entirely without them, their presence is all the more significant.

In JEFFREY's material of *Cunninghamia* the ray tracheids were found only on the side remote from the wound. In my material this was not the case, as they were often in direct contact with the traumatic canals. Of course, the position of the various traumatic series (see fig. 1) would indicate that the root had probably been wounded at different points on its circumference, and therefore even if JEFFREY's observation held good for this material, the ray tracheids ought to be found on any radius. However, in material of another species to be described immediately, such was distinctly not the case.

Let us now turn to the other species examined. A radial section of a wounded branch of *A. concolor* is shown in fig. 7. The short septated elements at the central part of the extreme left are part of the traumatic series. Following these on the margins of both rays are bordered-pitted elements which are obviously ray tracheids. The conditions existing in the wounded root of *A. amabilis* are thus exactly duplicated in the wounded branch of *A. concolor*. In both species the ray tracheids are often in line with parenchyma cells, as in fig. 7. The usual condition is the appearance of one or two parenchymatous cells in the summer wood and a similar number of ray tracheids conterminous with them in the first-formed spring

wood of the following year. Between these and the summer wood of the same year neither kind of element is to be found.

Another species in which ray tracheids were found is *A. homolepis*. Fig. 8 shows a ray in the region of the annual ring. On the upper margin are ray tracheids in line with a parenchyma cell. Fig. 12 is a more magnified view of these elements, and shows the bordered character of the pits more distinctly, especially of the two on the end wall. The material of *A. homolepis* is particularly interesting from the fact that it exhibited no trace of wounding either in radial or transverse sections. As the segment was of considerable length and contained ray tracheids throughout, the presence of the latter could scarcely have been the result of a distant wound, especially as there was no trace of traumatic canals. Their presence, therefore, must be considered as normal, or at least sporadic.

The only other species in which these structures were observed is *A. Veitchii*. Fig. 11 demonstrates their presence in this form, the bordered pit on the end wall being most distinct. The material was similar to that of *A. homolepis*, a branch which showed no trace of wounding. As in the other species, their typical position was in the spring wood following one or two parenchymatous cells in the summer wood of the previous year (see fig. 11).

Many other species were examined, including *A. lasiocarpa*, *Fraseri*, *Nordmanni*, *cephalonica*, *grandis*, *balsamea*, and *firma*, but none were found to have ray tracheids. A very diligent search was made in the case of *A. balsamea*, in which PENHALLOW reports having observed them sporadically. Normal and wounded roots, stems, branches, and seedlings, as well as witches' brooms, all failed to show a single indisputable ray tracheid. However, material collected during the active growing season and examined in the cambial region showed a slight border on the pits of some of the cells, which from their position were evidently doomed to degeneration in a manner to be described below.

In all those species in which ray tracheids were found, their position and association with neighboring cells were very suggestive. As has been described, they usually occurred in the spring wood, and were conterminous with one to several parenchyma

cells in the summer wood of the previous year (figs. 7, 8, 11). These groups of parenchyma cells at the boundary of the annual ring are characteristic features of many species of *Abies*. In the spring wood they disappear, to be revived again in the following summer wood. The result is the appearance of single cells or small groups of cells scattered along the margins of the rays, each group at the end of an annual ring. Between the groups there is usually no trace of cells, but here and there peculiar "ghostlike" appearances resembling cells may be seen. One of them is shown in fig. 6, which is a photograph of a section of *A. homolepis*. They are shadowy, structureless affairs, staining best in hematoxylon and giving no response to the phloroglucin test for lignin. Occasionally they form an almost continuous cell-like series from one group of parenchyma cells to the next, but usually they are rather isolated. That these structures are not merely thin sections of the sides of actual living cells is shown by their staining qualities, by their lack of structure, and by a study of a series of sections. The only explanation for their presence is that they are degenerated cells. In fact, it is possible to observe, especially in the cambial region, all stages in degeneration from such a conspicuous object as that seen in fig. 6, to ones which are barely discernible even with the strongest staining. The scattered condition is obviously due to the complete disappearance of some members of the series.

Now when ray tracheids occur, they identify themselves definitely with these series of degenerating cells. They may often be observed conterminous with one of the "ghosts." The inference seems irresistible that these "ghosts" were originally complete rows of ray tracheids which have degenerated in most species, but may survive sporadically in a few, and may be recalled traumatically in others.

The groups of parenchyma cells at the end of the annual ring are likewise definitely identified with these degenerating cells, whether ray tracheids are present or not. It seems probable that at the end of the year's growth, when there is a great demand for storage in preparation for the approaching winter, the cells which would otherwise degenerate are given a new lease of life and transformed into parenchyma cells which are capable of storage. That

the transformation has actually taken place is proven by the discovery of intermediate forms of cells. In fig. 10, which is a more magnified view of the lower part of fig. 8, is an element with a distinct bordered pit on its vertical wall and several equally distinct simple pits on its horizontal wall. This element, therefore, is neither a tracheid nor parenchyma cell, but combines the pitting of both. Several such cells were seen, in some cases both kinds of pits occurring on the same wall. So far as the writer is aware, the anomaly of bordered and simple pits occurring on the same element has never been observed except in this laboratory by Miss GORDON[4] in material of *Sequoia*.

A much commoner type of transitional element than the anomalous structures just described is illustrated in fig. 13, from *A. Veitchii*. The pits on the ray tracheid are so slightly bordered as to be scarcely distinguishable from the simple pits of the parenchymatous cells. The figure illustrates but one or two of the many forms intermediate between typically simple and typically bordered pits which may be observed on these elements.

Conclusions

The presence of ray tracheids as a result of wounding in *A. amabilis* and *A. concolor* parallels exactly the phenomena described by JEFFREY for *C. sinensis*. The interpretation advanced by him is that we have here a case of the revival by wounding of structures ancestrally present and lost in the course of evolution. Owing to the closer affinity of *Abies* with those genera in which ray tracheids are abundant, his reasoning applies with even greater force to the observations described in this paper. Again, their sporadic occurrence in uninjured material of a few species of the genus strongly supports this view. Further support is added by the association of the ray tracheids with the degenerating cells or "ghosts," and with the groups of marginal parenchyma cells at the ends of the annual rings. It may be concluded that ray tracheids were present in the ancestors of *Abies*, and have per-

[4] GORDON, MARJORIE, Ray tracheids in *Sequoia sempervirens*. New Phytol. 11:1–7. *figs*. 7. 1912.

sisted sporadically in a few species, but in the majority have either degenerated or been transformed to parenchyma.

Summary

1. Ray tracheids, marginal, interspersed, and elongated, were observed in association with wounds in *A. amabilis* and *A. concolor*.

2. They were also observed in uninjured material of *A. homolepis* and *A. Veitchii*.

3. Their usual position was in contact with a series of degenerated cells on one hand and a group of parenchyma on the other.

4. Transitions from ray tracheids to parenchyma were common, some elements having both bordered and simple pits, and others pits with borders of various sizes.

5. All the evidence points to ray tracheids being present in the ancestors of *Abies* and absent today by reduction.

The writer is indebted to Professor C. S. SARGENT for permission to collect material in the Arnold Arboretum, and to Mr. R. B. THOMSON for material and advice. The work was carried on under appointment as an "1851 London Exhibition Science Research Scholar" of the University of Toronto.

UNIVERSITY OF TORONTO

EXPLANATION OF PLATES XXIV AND XXV

PLATE XXIV

FIG. 1.—*Abies amabilis:* transverse section of wounded root, showing several series of traumatic resin canals; ×12.

FIG. 2.—The same: higher magnification, showing a row of traumatic resin canals; ×100.

FIG. 3.—The same: radial section; ×150.

FIG. 4.—The same: radial section, showing marginal ray tracheid with bordered pits in section; ×800.

FIG. 5.—The same: interspersed ray tracheid; ×1200.

FIG. 6.—*Abies homolepis:* radial section, illustrating the presence of "ghostlike" degenerated cell; ×400.

PLATE XXV

FIG. 7.—*Abies concolor:* radial section, showing wound tissue on the left and ray tracheids on the margin of both rays; ×500.

FIG. 8.—*Abies homolepis;* showing marginal ray tracheids; ×600.

FIG. 9.—*Abies amabilis:* showing vertically elongated ray tracheid; ×800.

FIG. 10.—*Abies homolepis:* showing element with both bordered and simple pits; ×800.

FIG. 11.—*Abies Veitchii:* showing presence of ray tracheid conterminous with parenchyma cell; ×600.

FIG. 12.—*Abies homolepis:* high power to show ray tracheid; ×1000.

FIG. 13.—*Abies Veitchii:* an element with pits very slightly bordered; ×600.

1

2

3

5

4

6

THOMPSON on RAY TRACHEIDS

7

8

10

9

11

12

13

THOMPSON on RAY TRACHEIDS

DO THE ABIETINEAE EXTEND TO THE CARBONIFEROUS?

ROBERT BOYD THOMSON AND ARTHUR EVERETT ALLIN

(WITH PLATE XXVI AND TWO FIGURES)

JEFFREY and CHRYSLER, in a recent monograph on the Pityoxyla of the Cretaceous (4), assign much importance to the presence of *Pityoxylon Chasense* in the Permian and to the supposed occurrence of *P. Conwentzianum* in the Carboniferous, as indicating the great geological age of the Abietineae. They state (p. 13):

The *Pityoxylon Conwentzianum* of GOEPPERT from the Carboniferous of Waldenburg, which has often been called in question, has received full confirmation from the description of a similar type of *Pityoxylon*, *P. Chasense*, by PENHALLOW, from the Permian of Kansas. In these two species vertical resin canals are said to be absent, although the horizontal canals of the fusiform rays are clearly present. There is, accordingly, every reason to believe that the Abietineae are a very ancient group in their first appearance. In fact, they may be traced geologically quite as far back as the Araucarineae, which it is customary at the present time to regard as the oldest of the Coniferales.

More recently GOTHAN (2) has again "called in question" the authenticity of *P. Conwentzianum* as a Carboniferous form. He shows that this species whose horizon was never determined cannot, on structural grounds, belong to the Carboniferous. In this regard he refers (1) to the modern character of the radial pitting of the tracheids, which he has shown (1) is entirely lacking in all true Carboniferous woods; and (2) to the typical annual rings which are present, which are not found in any Carboniferous form. He also refers to the doubt expressed by Count SOLMS as to the validity of *P. Conwentzianum*, and to the fact that no more material of it can be found in the Carboniferous of Waldenburg, from which much wood is known. Finally, he again emphasizes the uncertainty as to the source and horizon of the material, which he states was found "auf eine Halde (!) des Waldenburgischen" (2, p. 22). No reliance can thus be placed on this form as indicating the presence of the Abietineae in the Carboniferous.

P. Chasense was described by the late Professor D. P. PENHALLOW in 1900 from material which was collected by C. S. PROSSER

from the "Chase Formation (Permian) at Coon Creek, Chase Co., Kansas, in 1897" (PENHALLOW **5**, p. 76). The type set of sections is the property of the Peter Redpath Museum, and through the courtesy of the McGill authorities has been put at our disposal for study. It is to be regretted, however, that no more material of the specimen from which the sections were prepared can be found. Careful search has been made both at McGill and at Washington (U.S. Geological Survey), where PROSSER sent his collection. The sections are three in number, transverse, radial, and tangential. They are labeled "*Pityoxylon Chasense*, 5, Cretaceous,[1] C. S. Prosser." Plate figs. 1–3 show these at a low magnification. The matrix is siliceous, but the material is only "fairly well preserved," and though the sections have been excellently made, certain important structural features are not determinable. PENHALLOW'S description is very brief, and is not illustrated. This renders it difficult to correlate it with the sections.

The transverse section is 12.5 mm. in radial extent, and in that distance shows no growth rings, so that it seems probable that these are absent or at least poorly developed, as PENHALLOW has stated. This feature and the form and arrangement of the tracheids are shown in plate fig. 4. The absence of annual rings is not a characteristic of the genus *Pityoxylon* of KRAUS, and yet in spite of this, and in spite of other important features which indicate its cordaitean affinity, PENHALLOW placed this form under that genus, because of the occurrence of what he considered were horizontal resin canals.

Text fig. 1*A* illustrates the character of the medullary ray cells in radial section. They are four to five times as long as high, and, as compared with the tracheids, are thin-walled; the radial extent of the latter and the thickness of their walls are indicated by the sets of short lines below the parenchyma cells. Many rays were examined, but no pits could be found on either the horizontal or terminal walls, nor is there any special thickening of these walls, features which are characteristic of *Pityoxylon*. Their structure, on the contrary, is of the characteristic cordaitean or *Araucarioxylon* type.

[1] There would seem to have been an error in labeling these "Cretaceous," since the Chase formation is Permian, as PENHALLOW himself has stated in his description.

The radial pitting of the tracheids is illustrated in text fig. 1*B*, which is taken from the radial section at the place marked *d* in plate fig. 2. The bordered pits are "in 1–3 rows, chiefly 2 rows."[2] They are alternate in arrangement, and flattened, as it were, by mutual contact, often presenting a more or less hexagonal outline. The orifice is not "probably round," however, though such appearances are quite common where the preservation is defective (text fig. 1*C*).

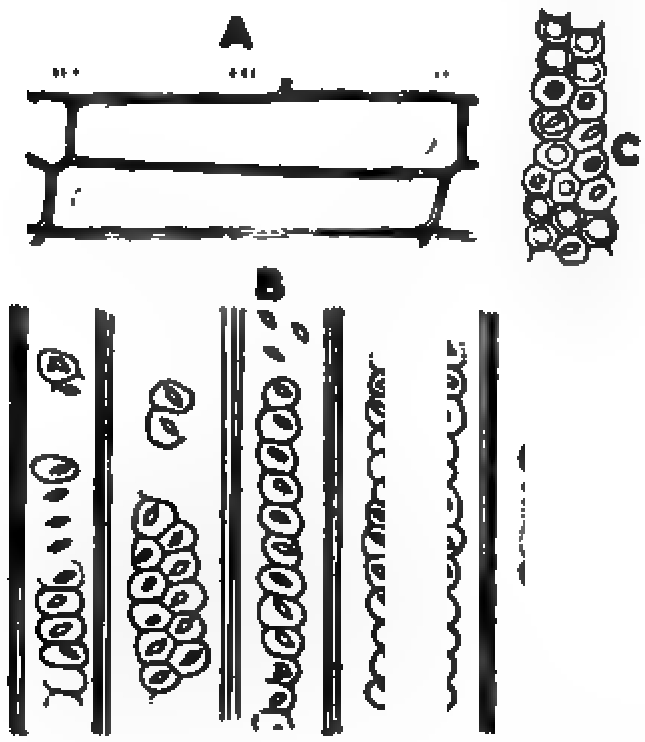


FIG. 1 FIG. 2

FIGS. 1–2.—Fig. 1, from radial cross-section: *A*, medullary ray cells; *B*, radial pitting of tracheids (from plate fig. 2 at *d*); *C*, radial pitting in poor state of preservation; ×250; fig. 2, from tangential section (plate fig. 3 at *a*): showing tissue continuous and also tangential pitting adjacent to the ray; ×100.

Even here transitions to the normal type can be observed. It is elongated and obliquely placed, the two orifices on contiguous walls in some cases showing at right angles to one another (first and second tracheids from the right in text fig. 1*B*). This is not the character of the radial pitting of *Pityoxylon* as defined by KRAUS (SCHIMPER and SCHENCK **6**, p. 852), "Aréoles unisériées; opposées lorsqu'il y en a deux rangs," but that of an *Araucarioxylon* or cordaitean form.

The presence of horizontal resin canals upon which "*P. Chasense*" is referred to the genus *Pityoxylon* is exhibited, according

[2] Fifty counts were made in different parts of the radial section with the following result: 1-seriate 16 per cent, 2-seriate 62 per cent, and 3-seriate 22 per cent.

to PENHALLOW, "in the tangential section only, probably in consequence of the special condition of preservation," though what that "special condition" may be when the sections are all made from the same block is not evident. This feature, however, is considered important enough, in spite of the above described cordaitean features, to "separate the plant from *Cordaites*, and its affinities are rather with the *Pityoxylon* of KRAUS."

In the tangential section there are four broad medullary rays (plate fig. 3, *a*, *b*, *c*, *d*) with their tissues in a fair state of preservation, the two best preserved of which are shown in figs. 6 and 7. There are also traces of two more. PENHALLOW's description of these is "fusiform rays, the terminals linear and of the structure of the uniseriate rays; the central tract very broad, nearly round; the cells large, thin-walled, irregular, and enclosing a small central resin passage with large epithelium cells." The writers have examined all these rays carefully, and the sketch (text fig. 2) was made after a prolonged study of the best preserved one (fig. 6). The camera lucida was used to outline this, but a few details were added afterward. It shows the tissue continuous from side to side of the ray, neither could there be found in this nor in any of the others a trace of a "small, central resin passage with large epithelium cells." Fig. 7 shows the only one that could be considered to have anything resembling a resin canal in it, and it was found by the use of the polariscope that the two darker areas (*a* and *b*) in this were due to aggregates of crystals of silica. Partial outlines of the crystals appear in the photograph.

Since the writers could find no evidence of resin canals in these large fusiform rays, it became interesting to know their real character. A significant feature in this connection is the irregularity of their margin, which is very different from that found in rays in the pines with horizontal resin canals, or even in such abnormal cases as those of *Sequoia Penhallowii* (JEFFREY 3). Around the rays, moreover, there is a considerable amount of tangential pitting on the tracheids (text fig. 2), a feature which is not found in any form known to the writers in connection with rays which inclose resin canals. This, however, is a feature of medullary rays which contain leaf traces, and since we have found undoubted leaf

traces in the radial and transverse sections of *P. Chasense* in rays which are quite similar in size and structure to those in the tangential section (cf. plate figs. 6 and 7 with fig. 8), it is considered that these are identical with the fusiform rays described by PENHALLOW. In the radial section they pursue an almost horizontal course (plate figs. 2*a* [?] and *b*), as is the case in the old wood of the Araucarineae. Further explanation need not be entered into here, since one of the writers is preparing a contribution to the character of the leaf trace in certain fossil and living conifers, in which this feature will be studied in detail.

Since, then, the so-called resin canals of "*Pityoxylon Chasense*" are proven not to be such, there is left no basis for calling this form a *Pityoxylon*. On the other hand, (1) the absence of annual rings, (2) the character of the ordinary medullary rays (1 to partly 2-seriate with cells of thin-walled unpitted parenchyma), and (3) the multiseriate, alternate, and hexagonal radial pitting of the tracheids afford clear indication of its cordaitean affinity. This form, then, instead of affording "full confirmation" (*op. cit.*, p. 1) of the authenticity of *P. Conwentzianum*, lends no support to it, but might rather be considered as emphasizing the insecurity of the evidence upon which, as GOTHAN has recently shown (see p. 1), the latter is referred to the Carboniferous. The claim for the great geological age of the Abietineae thus fails on critical study of both the Permian and the Carboniferous forms upon which it is based.

UNIVERSITY OF TORONTO

LITERATURE CITED

1. GOTHAN, W., Die fossilen Hölzer von Konig-Karls-Land. Kungl. Svensk. Vetensk. Akad. Handl. **42**: no. 10. 1907.
2. ———, Die fossilen Holzreste von Spitzbergen. *Ibid.* **45**: no. 8. pp. 56. *pls. 7.* 1910.
3. JEFFREY, E. C., A fossil *Sequoia* from the Sierra Nevada. BOT. GAZ. **38**: 321–332. *pls. 18, 19.* 1904.
4. ———, and CHRYSLER, M. A., On Cretaceous Pityoxyla. BOT. GAZ. **42**: 1–15. *pls. 1, 2.* 1906.
5. PENHALLOW, D. P., North American species of *Dadoxylon*. Trans. Roy. Soc. Canada. II. **6**[4]: 51–97. *pls. 9.* 1900.
6. SCHIMPER and SCHENCK, Paléophytologie: Part II of ZITTEL's Traité de Paléontologie. Paris. 1891.

DESCRIPTION OF PLATE XXVI

FIG. 1.—Transverse section in two parts (*a* and *b*); ×5.

FIG. 2.—Radial section: at *a*, a possible branch; at *b*, a leaf trace cut longitudinally; at *c*, one cut obliquely; and at *d*, the pitting shown in text fig. 1*C;* ×5.

FIG. 3.—Tangential section: *a, b, c, d* are the fusiform rays; ×5.

FIG. 4.—Transverse section: showing tracheids and medullary rays with no annual rings; the figure is from three photographs combined; ×80.

FIG. 5.—Radial section of medullary rays; ×40.

FIG. 6.—Tangential section of best preserved medullary ray (*a* in fig. 3) from which text fig. 2 was drawn; ×80.

FIG. 7.—Tangential section of a medullary ray (*d* in fig. 3) with two aggregates of crystals of silica in it at *a* and *b;* ×80.

FIG. 8.—Radial section of the leaf trace, from fig. 2*b;* ×40.

1

8

THOMSON & ALLIN on PITYOXYLON

BRIEFER ARTICLES

SUSAN MARIA HALLOWELL

(WITH PORTRAIT)

Susan M. Hallowell was born in Bangor, Maine, on August 25, 1835, and died December 15, 1911, at Wellesley, Massachusetts. From childhood Miss Hallowell loved study and was a lover of nature. She began her profession of teaching as soon as she was graduated from the high school. At that time institutions for the higher education of women were unknown. For more than twenty years she taught in the Bangor high school, continuing, as best she could, her self-education. But her thirst for knowledge could not be thus slaked. She longed to come into touch with the great masters of thought, and so, while still a teacher in the high school, she found her way into the laboratories of Agassiz and of Asa Gray. These educators recognized the rare genius and power of this young woman, and it was through their recommendations that, in 1875, she was appointed Professor of Natural History in Wellesley College almost before the corner-stone of the first building of the new college was laid.

With that indefatigable zeal so characteristic of her whole life, she began the work in preparation for the new position. She went from college to college, from university to university, studying the scientific libraries and laboratories. At the close of this investigation she

announced to the founders of the college that the task which they had assigned her was too great for any one individual to undertake. There must be several professorships rather than one. Of those named she was given first choice, and when in 1876 she opened her laboratories and actually began her teaching in Wellesley College, she did so as Professor of Botany, although her title was not formally changed until 1878.

As soon as the newly founded department could be spared her immediate guidance, she went to Europe for further study. Here again she found the universities closed to women students. In that quiet but persuasive manner so characteristic of her, she applied for admission to the University of Berlin, and was the first woman to be admitted to the botanical lectures and laboratories of that university. At the age of 67, Miss HALLOWELL retired from active service in the college and was made Emeritus Professor of Botany, in February 1902.

Professor HALLOWELL was a pioneer in the higher education of women, the first and only woman to have organized and maintained at a high degree of efficiency, for more than twenty-five years, a department of botany. The foundations which she laid were so broad and sure, the several courses which she organized were so carefully outlined, that, except where necessitated by more recent developments in the science, only very slight changes in the arrangement and distribution of the work in her department have since been necessary. In addition to the providing of general equipment of the laboratories, much time was devoted to the development of the herbaria and to the securing of other illustrative material. She organized and built up a botanical library which from the very first was second to that of no other college in the country, and is today only surpassed by the botanical libraries of a few of our greatest universities. With an enthusiasm that never failed, and a persistence that knew no defeat, she gave herself to the working out of her ideals in scholarship and in life.

Gentle and dignified in manner, sympathetic and generous of heart, rich in her knowledge of nature, with a rare felicity of expression, and with that humility and reverence which characterize the true lover of nature, she inspired and enriched the lives of her pupils and associates.

Professor HALLOWELL was not a productive scholar, as that term is now used, and hence her gifts and her achievements are but little known to the botanists of today. She was pre-eminently a teacher and an organizer. Only those who knew her in this double capacity can fully realize the richness of her nature and the power of her personality. Her work will not be immortalized in cold bibliographies, neither will it be

writ alone in the hearts of those for whom and with whom she labored, for she touched life to nobler issues. With her death there has passed from us another of that constantly diminishing group of rare students and teachers who have contributed so largely to the dignity and permanency of higher education in America.—MARGARET C. FERGUSON.

TWO EPIPHYTIC ALGAE: A CORRECTION

Mr. J. H. BARNHART, through the editor of the BOTANICAL GAZETTE, has called attention to a possible difference in opinion in regard to the correctness of the name *Pirulus gemmata* given to a new genus of algae described in this journal.[1] When the name was selected, the writer was aware of this possible difference in interpretation, but the form was chosen which seemed to her to be most appropriate. On submitting the question to several authorities, however, the consensus of opinions seems to be that the name should read **Pirula gemmata** instead of *Pirulus gemmata*, and the writer would like to make this change.

Attention was also called by Mr. BARNHART to a mistake in the name *Aeronema polymorpha*, which should read **Aeronemum polymorphum.**—JULIA W. SNOW, *Smith College, Northampton, Mass.*

[1] SNOW, JULIA W., Two epiphytic algae. BOT. GAZ. 51: 360–368. *pl. 18.* 1911.

CURRENT LITERATURE

BOOK REVIEWS

British vegetation

In two respects, at least, the appearance of *Types of British vegetation* marks an epoch in the development of plant geography.[1] In the first place, the publication of the volume at this time is due to the organization of an International Phytogeographic Excursion in the British Isles during the summer of 1911. The volume was prepared in anticipation of this excursion, and advance copies were presented to the members of the party. The chief result of this excursion has been to internationalize for all time the subject of plant geography, and to divest it of the provincialism which has hitherto too greatly characterized it. Besides marking the initiation of internationalism in phytogeography, this volume marks another great advance, namely, the study of vegetation by an organization rather than by an individual. While edited by TANSLEY, the volume was gotten together by the "Central Committee for the survey and study of British vegetation," more popularly known as the "British vegetation committee." It is not so long ago that the study of vegetation played an insignificant part in British botany. Through the work of their vegetation committee, the British not only have caught up with their American and continental brethren, but, in organization at least, they have forged ahead.

The introduction deals with the units of vegetation, following the general lines marked out previously by MOSS.[2] While all plant geographers seem to believe in the reality of the terms formation and association, and to believe that the formation should be used as the larger unit, including various smaller units or associations, it is evident from this book, as from the discussions of the 1911 excursion, that the British plant geographers differ radically from all others in the practical application of these terms. For example, calcareous soils are regarded as having a single formation, which includes such diverse things as limestone-pavement associations with almost bare rock surface, limestone grassland, limestone scrub, chalk heath, yew woods, ash woods, and beech woods. Similarly the sand-dune formation is composed of strand associations, morrain-grass and couch-grass associations, dune grassland, dune scrub with willows, and dune marshes. The reviewer has shown that on the sand dunes of Lake Michigan there is to be found nearly every kind of plant formation characteristic of the region, from the xerophytic vegetation of the

[1] TANSLEY, A. G., with various collaborators, Types of British vegetation. pp. xx+416. *pls. 36. figs. 21.* Cambridge: University Press. 1911.

[2] See BOT. GAZ. 52:321. 1911.

moving dunes or the swamp vegetation of the dune depressions to a mesophytic climax forest of beech and maple. By the British concept all of these are to be considered as composing a single formation! It must be admitted that the British concept of formation is the most workable yet proposed, for it represents in essence the aggregate of plant associations which compose a successional series on a given habitat. It must be admitted also that those who oppose the British concept are not agreed among themselves, when it comes to actual field discriminations between associations and formations. However, the British concept proposed by Moss and adopted by the committee, represents a most radical departure from all past formational concepts, and seems to be out of harmony with the proposals internationally agreed upon in Brussels in 1910.

Whatever may be said concerning concepts and modes of classification, nothing but praise can be rendered for the detailed presentation of British vegetation. The editor presents the chapter on British climate, as well as a part of that on the soil; W. G. SMITH gives the part on Scottish soils, and G. A. J. COLE that on Irish soils. Following a description of the general distribution of British vegetation by the editor is an account of the plant formation of clays and loams, also by the editor. The chief association here is that dominated by *Quercus pedunculata*, with an undergrowth dominated by the hazel. This formation includes also retrogressive associations of scrub (dominated largely by Rosaceae) and grassland. The editor contributes also the chapter on the formation of sandy soil. The chief association is that of oakwood, in which *Q. sessiliflora*, as well as *Q. pedunculata*, is a prominent member. The chapter on the heath formation is presented as a whole by the editor, the part on Scottish heaths being contributed by W. G. SMITH. As was well shown at various points in the 1911 excursion, the heath often has originated retrogressively through the degeneration of woodland. The first step in such retrogression appears to be the invasion of oakwood by birch and heather; after a time the heath may become dominant. The heath in time may be invaded by pine or birch, illustrating progressive succession.

Most of the chapter on formation of the older siliceous soils is contributed by Moss. The chief association is an oakwood dominated by *Q. sessiliflora*. Retrogression from forest through scrub to grassland is well illustrated in this formation. The splendid oak woods of Killarney, with their Mediterranean components, notably *Arbutus Unedo*, are classed here; the Killarney forest proved to be one of the most fascinating areas visited by the 1911 excursionists. In the preparation of the extensive and interesting chapter on the formation of calcareous soils, the editor was aided by Moss and also by W. M. RANKIN. Three subformations are here recognized, that of the older limestones, that of the chalk, and that of the marls and calcareous sandstones. The first is presented by Moss, who also conducted the excursion to the Derbyshire dales, where it is well illustrated. The chief association is dominated by the ash, *Fraxinus excelsior*, and retrogressive stages to scrub and later to

grassland are frequently observed. A remarkable association is that of the limestone pavements, such as the 1911 party visited in western Ireland; these areas have much bare rock surface, and a most interesting vegetation, largely mesophytic, is all but hidden in deep crevices. The chalk hills or downs, while resembling the older limestones, are characterized more by beech woods than by ash woods, though the latter are sometimes found. Another interesting type of the chalk is the yew woodland.

The chapter on aquatic vegetation is by the editor, except for the part on the plankton, which is contributed by G. S. WEST, and the part on quickly flowing streams, which is contributed by MOSS. Short chapters follow on the marsh formation and on the vegetation of peat and peaty soils, both by the editor. Miss PALLIS, the efficient guide of the 1911 excursion in the Norfolk Broads, contributes a chapter on the aquatic and fen formations of that region. This chapter presents a district as a unit, the consideration of the physiographic development of the area being followed by a treatment of the aquatic formation and the fen formation with its various associations, and by a discussion of the genetic relationships of the associations involved.

Two chapters are devoted to the moor formation, the lowland moors being presented by the editor, assisted by RANKIN, and the upland moors by F. J. LEWIS, C. E. MOSS, and W. G. SMITH. RANKIN, who conducted the 1911 party to some of the Lancashire moors, considers the latter under the two heads of estuarine and lacustrine moors, the former being much the more extensive. While the heather, *Calluna vulgaris*, generally dominates the successional series, here it seems to culminate in a birchwood, but there are many examples of retrogression to heather moorland with birch stumps buried *in situ*. RANKIN considers also the valley moors of the New Forest, which were visited from Portsmouth at the close of the excursion. Upland moors were seen frequently during the course of the excursion, the foreign guests being repeatedly surprised at their vast extent, especially in habitats which in most parts of the world would be forested. That these were once forested, at least in part, was made evident again and again by the discovery of forest layers buried in the peat. Over vast areas the dominant plant of the upland moors is a cotton grass, *Eriophorum vaginatum*. In some places, especially in Scotland, there are extensive grass moors. Denudation and retrogression are frequently conspicuous.

The chapter on arctic-alpine vegetation is presented by W. G. SMITH, who was the chief guide of the party in Scotland. The discussion is devoted chiefly to Ben Lawers, which was visited by the excursionists. The delimitation of formations here is more in harmony with that employed by most writers, the author distinguishing three formations near the summit: the arctic-alpine grassland formation, the formation of mountain top detritus, and the formation of arctic-alpine chomophytes (i.e., plants of rock ledges and fissures). The final chapter, prepared chiefly by the editor, considers the vegetation of the sea coast, the chief formations recognized being the salt

marsh and the sand dune. The composition of the various associations and the trend of succession are like those of the Continent and are familiar through the work of WARMING, MASSART, and other writers. Perhaps the most unique feature of the British coast is afforded by the shingle beach communities, which are most ably treated by OLIVER, who conducted the 1911 party to his seaside laboratory at Blakeney, where these communities are well developed. The most striking feature here is the presence of a shingle or gravel dune, which invades the marshland and presents conditions resembling in many ways the more familiar phenomena of sand dunes.

The photographic illustrations in this volume are notably well selected, and most admirably reproduced, and are supplemented by a few instructive diagrams. The British vegetation committee may well be proud of their record for 1911. It is to be hoped and expected that such books as the one here reviewed, and such phytogeographic excursions as the one here mentioned, will hereafter be frequently recurring features of phytogeographic progress.—H. C. COWLES.

The soil solution

Those plant physiologists who are interested in the subterranean surroundings of plants and in the relations which obtain between soil conditions and plant activity will welcome CAMERON's little book entitled *The soil solution*.[3] The treatment is exceedingly clear and concise, logically arranged, and very readable. Furthermore, it is unquestionably the best and most scientific treatise on this difficult yet most important subject which we have seen. The author originally approached the soil problems from the standpoint of the chemist, developing their biological and agricultural aspect according to the demands of researches under his direction, and perhaps this fact has left a mark upon some of his discussions which may seem novel to the reader coming to this field from a specifically botanical training. But the novel features of the author's treatment may be regarded as quite in line with the recent trend of physiology toward a quite uncolored physical treatment.

Another group of workers whose attitude toward plant happenings is often not that of the physiologist, and whose activities have been mainly directed toward the empirical acquisition of more or less superficial principles and relations, will read CAMERON's contribution with much interest, perhaps even with excitement. We refer here to students of practical agriculture, who will find here that some of the most widely accepted hypotheses of this field are clearly discredited. This will not be at all surprising, however, to him who has followed the recent literature, for the previous publications of the author and his colleagues have given, from time to time, the main features of the researches upon which his present attitude toward soil science has been built up. During

[3] CAMERON, FRANK K., The soil solution, the nutrient medium for plant growth. pp. v+136. *figs. 3.* Easton (Pa.): The Chemical Publishing Co. 1911.

the past decade we have received many quite novel propositions and suggestions from this group of workers, most of which were read with greater or less lack of conviction by agricultural scientists. With the advance of time, however, most of these new ideas have continually gained ground throughout the world.

Aside from its general value as an example of an exceptionally rational study of a very complex and difficult set of natural relations, the keynote of the present book is perhaps suitably expressed by the following sentence taken from p. 17: "Just as the phlogiston theory passed away when the elementary nature of oxygen was established and LAVOISIER taught the scientific world to use the balance, so the plant food theory of fertilizers must pass with increasing knowledge of the relation of soil to plant and the application of modern methods of research to the problem."

It is emphasized throughout that the problems here involved are dynamic; that the soil, as well as the plant, are the seats of continuously changing chemical and physical processes; thus no static interpretation of the environment of roots is of much avail, and the general failure of soil analyses to answer the fundamental question with which we are concerned seems to have been due to the failure of such methods to bring out the dynamic nature of soil phenomena. A chapter is devoted to a somewhat thorough discussion of the concentration and the nature of the mineral solutes of the soil solution, with reference to the conditions which control these features and keep them in constant change, always tending toward equilibrium but probably seldom attaining it. Then follows a discussion of soil absorption, with a clear setting forth of the logical fallacy of the prevalent interpretation of apparent soil acidity.

In the chapter on "The balance between supply and removal of mineral plant nutrients," MCGEE's startling series of terms ("run-off," "cut-off," "fly-off") to denote the superficial and subterranean drainage and the loss by evaporation, respectively, from the soil has been adopted. The reviewer can see so little tendency of modern serious English to revert to this fundamentally Teutonic style of etymology that he cannot but look askance at these last two newly coined expressions. This chapter is the weakest in the book, and most readers will feel that the question "Is the movement of mineral plant nutriments toward the surface soil equal to or in excess of the removal by drainage waters and garnered crops?" (p. 75) is not answered with data or considerations which even "appear sufficient for the present purpose." The approximations given of the number of tons of potassium, etc., annually carried, in the United States, toward the soil surface, removed by crops, and washed into the sea are of no interest as regards any particular plant or soil. The question must be settled with reference to particular soil areas, by experimental studies yet to be accomplished. However, the author is quite aware of the weakness of these calculations, and admits that "it is wise to avoid giving them too much emphasis." His thesis against the LIEBIG theory of fertilizer action gets its support from quite different lines of argument.

In the chapter on "The organic constituents of the soil solution" is given a convincing account of the toxic substance theory of soil fertility. Any treatment of an organically poisoned soil, which will increase its absorptive properties or its oxidizing power seems to have a beneficial effect upon plants growing therein. The commonly used fertilizer salts are often effective in this way, so that there is nothing in the new theory which might lead one *not* to use the ordinary fertilizers prescribed by the "plant food" theory. This more recent finding of the Bureau of Soils makes the violent and often personal attacks, that have been calculated to hinder the progress of these investigations, appear largely as the mere pommelling of a man of straw.

The book ends with a chapter on the phenomena of alkali soils, dealing with the development of alkali and the theory of its practical handling.—B. E. LIVINGSTON.

Fossil plants

In the second volume of his *Fossil plants*, Professor SEWARD[4] continues the work begun over ten years ago and apparently destined to become truly monumental. It is to be hoped that his anticipation of the early appearance of the third volume on the gymnosperms may be realized, and that a fourth hinted at, rather than promised, which is to deal with the angiosperms, may likewise soon be published. The author brings very unusual qualifications to the titanic task of writing a comprehensive textbook of the present condition of our knowledge of fossil plants in both their botanical and geological bearings. He possesses in an unusual degree an acquaintance with the older paleobotany, dealing mainly with the superficial features of plants as seen in impressions, and at the same time is thoroughly in touch with the modern development of the subject, which has put the study of internal structure in the foreground. It is to be regretted that some of the younger investigators of fossil plants are often deplorably ignorant of the older point of view. SEWARD certainly does not err in the direction of the neglect of the older literature or superficial features, which in many cases constitute the only evidence available. Another advantage enjoyed by the author is his unique first-hand knowledge of the material treated. By his travels to various paleobotanically interesting regions and by personal visits to most of the important European collections, he has acquired an intimate acquaintance with fossil plants in their fullest systematic, geological, geographical, and evolutionary bearings possessed by no other living paleobotanist.

The present volume continues the treatment of the Pteridophyta begun in the first, which appeared over ten years ago. In the preface he points out the happy circumstance that recent activity has been chiefly in the field of the present volume, and that as a consequence the first is little out of date. Beginning with a continued discussion of the Sphenophyllales, the writer subscribes a very

---

[4] SEWARD, A. C., Fossil plants. Vol. II. pp. xxii+ Cambridge: The University Press. 1910.

qualified adherence to the views expressed in recent years in England, as to the affinity of the Psilotales with this phylum. The genus *Psilophyton*, established by the late Sir WILLIAM DAWSON of McGill University, for forms from the Devonian of eastern Canada and of Scotland supposed to be allied to the living *Psilotum*, is critically examined and rejected as being based on insufficient evidence.

The Lycopodiales are considered in 250 well-illustrated pages. Beginning with the superficial and anatomical characters of the living representatives of the group, the author, in common with all paleobotanists of standing, rejects the idea that the genus *Isoetes* has filicinean rather than lycopodineous affinities. This suggestion, first made by an English plant physiologist, seems now to be finally disposed of. The fossil Lycopodiales are discussed under the convenient captions of Isoetaceae and Pleuromeia, herbaceous fossil Lycopodiales, and arborescent Lycopodiales, a special chapter being added on those remains which the author frankly designates seed-bearing Lycopodiales.

The Filicales or fernlike Pteridophyta, together with a number of apparently allied forms, concerning which it is yet uncertain whether they are true ferns or merely fernlike seedplants, occupy the remaining and larger part of the volume. The treatment of the fossil Filicales begins with a comprehensive anatomical and systematical account of their still living allies. The anatomical treatment, as might be expected, is characterized by a decided "insularity," the views of GWYNNE-VAUGHAN, BOODLE, and other English anatomists being unhesitatingly adopted. The chapters on fossil ferns contain such a well-digested wealth of material that it is quite impossible to summarize them or even indicate their tendency in this necessarily brief review. It is enough to say that they constitute a particularly valuable part of the present volume and represent a region of the fossil field where the author is peculiarly at home.

If the work of which the volume under consideration constitutes such an important fraction is completed, as is devoutly to be desired, it will be the most complete and thoroughly modern work on the subject, and will serve to replace the now somewhat antiquated botanical part of ZITTEL'S well-known *Handbuch*, compiled by SCHIMPER, SCHENK, KRAUS, and others. It is lightened and vitalized by the comparison of external and internal features of the various fossils treated, with the similar forms still living. By this method the reader, whether he be botanical or geological in his interests, acquires a vivid picture of the evolutionary sequence of plants in the history of our world.—E. C. JEFFREY.

MINOR NOTICES

Bulletin du Jardin botanique de Buitenzorg[5] is the title resumed by the Botanical Gardens of Buitenzorg to take place of the well-known serial "Bulletin du Département de l'agriculture aux Indes néerlandaises." The

[5] Bulletin du Jardin botanique de Buitenzorg. Deuxième série. No. I, pp. 29, *pls. 4*, August 1911. No. II, pp. 29, October 1911.

two numbers issued recently contain articles on Malayan ferns and Papuan orchids by eminent specialists. Several of the species included are new to science.—J. M. GREENMAN.

Handbook of deciduous trees.—The eleventh part (sixth section of second volume) of SCHNEIDER'S *Handbook* has appeared,[6] following the preceding part in the same year. As stated in preceding notices, it contains descriptions, with illustrations, of the angiospermous trees of central Europe, both native and under cultivation. The present part begins with the completion of *Viburnum* and ends with *Fraxinus*.—J. M. C.

Flora of Jamaica.[7]—Of the numerous publications concerning West Indian botany which have appeared in recent years, it is doubtful if any has combined so successfully a scientific and semipopular treatment as the present volume. It concerns the Orchidaceae only, and is the result of years of observation of living plants, supplemented by the study of a large amount of herbarium material, particularly the collections in the British Museum, in the Kew Herbarium, and in the Herbarium of the government of Jamaica.

The total number of genera constituting the orchid flora of Jamaica is given as 61, and to these are referred 194 species. One genus, *Homalopetalum*, and 73 of the recognized species are said to be confined to the island. The strongest affinity of the orchid flora is said to be with Cuba, as shown by the fact that 82 out of the 121 species, which are not endemic, occur in Cuba, and 14 of these are restricted to the two islands. The book is attractive in appearance, the keys concise, the synonomy ample but not cumbersome, the descriptions clear, and exsiccatae are very fully cited; moreover, the text is amplified by 32 full-page plates, illustrating all the genera represented, so that the book will be helpful to those interested only in living orchids, as well as to those occupied with the study of herbarium material. The authors state "it is proposed that the present volume shall form the first part of a complete *Flora of Jamaica*." It is earnestly hoped that the proposed work may be carried to completion.—J. M. GREENMAN.

New England trees in winter.—Books of a popular or semi-scientific type dealing with our native trees are already more than sufficiently abundant, and yet it is safe to say that the present volume by BLAKESLEE and JARVIS[8]

[6] SCHNEIDER, C. K., Illustriertes Handbuch der Laubholzkunde. Elfte Lieferung (sechste Lieferung des zweiten Bandes). Imp. 8vo. pp. 657–816. *figs. 420–514*. Jena: Gustav Fischer. 1911. *M* 5.

[7] FAWCETT, WILLIAM, and RENDLE, ALFRED BARTON, Flora of Jamaica, containing descriptions of the flowering plants known from the island. Vol. I. Orchidaceae. 8vo. pp. xviii+150. *pls. 32*. London: British Museum (Natural History). 1910.

[8] BLAKESLEE, A. F., and JARVIS, C. D., New England trees in winter. Storrs Agricultural Exper. Sta. Bull. 69. pp. 269. *pls. 109*. 1911.

will be welcomed on its merits both by botanists and by the general public. It consists of an introduction of an elementary character discussing the general problems of tree growth and illustrating some of the technical terms employed, a key for the determination of species on the basis of leaf and bud characters, supplemented by additional keys for the chief genera, and illustrated descriptions of over 100 species found in New England. This list includes not only all that are native to the region, but in addition the species that are commonly grown for ornamental purposes, thus extending the usefulness of the volume to the study of the trees of city parks and of areas far beyond the limits designated in the title of the volume.

One page is devoted to the description of each tree, while facing the description is a plate illustrating the species in winter condition. These plates contain reproductions of photographs of the general habit, the trunk, showing bark characters, the twig with buds and leaf scars, and the fruit. They are so uniformly excellent in quality that they must be regarded as the best collection of illustrations of the sort that have yet appeared. By their aid almost all common trees may be recognized readily by the ordinary reader. The descriptive text is wonderfully complete when its brevity is considered. Synonyms of both popular and scientific names are given, followed by separate paragraphs on the habit, bark, twigs, leaf scars, buds, fruit, wood, distribution, and comparisons with other species. Such an arrangement of material makes the manual well adapted for ready reference. As a manual it should be a valuable addition to those already available for college classes, but it is likely to prove even more valuable to teachers in public and high schools who are attempting to lead pupils to become familiar with our native trees. In addition to its present form, its authors indicate their intention of publishing it as a book, thus making it more widely available.—GEO. D. FULLER.

British liverworts.—In the prefatory note to a little volume on liverworts[9] the authors say that the book is intended to be a companion volume to their essay on *British mosses*. It is sincerely hoped that it will always remain on the shelf with that volume, and not fall into the hands of isolated students who are trying to get accurate information about liverworts. A few quotations will show what the authors know about the group as well as botany in general. "The liverworts present to one's mind the idea of a crowd of organisms which have not made up their minds in which line they shall go, and are trying experiments in all directions to see what is best for them to take." The following statement will be interesting to morphologists and physiologists: "A marked peculiarity of the thallus [of *Anthoceros*] is found in the manner in which the coloring matter is disposed. In some cells the chlorophyll may be seen gathered round the cell walls, either forming a continuous line or as separate

[9] FRY, EDWARD and AGNES, The liverworts, British and foreign. pp. viii+74. *figs. 49*. London: Witherby & Co. 1911.

bodies, but other cells, instead of possessing many diffused grains of chlorophyll, have a so-called chloroplast, a large flattened plate of coloring matter which incloses the nucleus." Of *Marchantia* we read: "Below and between each pair of rays the disk bears a perichaetium, i.e., the wrapper or involucre of a sporogone or female cell, which when fertilized by an antherozoid produces a mass of cells accompanied by elaters. The archegone itself thus becomes the spore case. These female organs are variously known as disks, receptacles, or inflorescences." Again, "On the upper surface of the thallus of *Pellia* may be seen, in both spring and autumn, small dots on either side of the midrib. These are very minute globular bodies attached by a slight thread to the subadjacent tissue. These bodies are known as antheridia or antherids, and may be compared with the stamens of flowering plants. From each antherid comes at maturity a mass of small spiral bodies, known as antherozoids (or spermatozoids), which may be compared with and play the part of the pollen of a flowering plant." Using *Pellia epiphylla* as an example, we find that "if we start with a spore, we shall find that it produces a thallus on which grow the archegones and the antherids, which by their union produce a fertilized ovum." There are many more such statements in the little book.—W. J. G. LAND.

NOTES FOR STUDENTS

Current taxonomic literature.—S. ALEXANDER (Rep. Mich. Acad. Sci. **13**:191–198. 1911) records the results of a continued study of the perennial species of *Helianthus*. The author finds distinguishing characters in the underground parts of sunflowers and incorporates these characters in a tabular synopsis of the Michigan species.—G. BEAUVERD (Bull. Soc. Bot. Genève II. **3**:253–260. 1911) under the title "Contribution a l'étude des Composées" has proposed a new genus (*Parantennaria*) founded on an Austrian species, *Antennaria uniceps* F. v. Müller.—O. BECCARI (Philip. Journ. Sci. Bot. **6**:229, 230. 1911) gives a list of plants of the island of Polillo, describing a new species of *Livistona* (*L. Robinsoniana*) and two new varieties in the genus *Areca*.—E. P. BICKNELL (Bull. Torr. Bot. Club **38**:447–460. 1911) in an eighth article on "The ferns and flowering plants of Nantucket" records further noteworthy plants and characterizes a new species of *Amelanchier*.—G. BITTER (Bot. Jahrb. **45**:564–656. *pls. 4–10.* 1911) has published a revision of the South American genus *Polylepis*, recognizing 33 species, 14 of which are new to science; the group has its greatest specific diversity in the north Andean region.—N. E. BROWN (Bot. Mag. *t. 8402.* 1911) describes and illustrates a new species of *Cladium* (*C. pubescens*) from Peru.—E. B. COPELAND (Leafl. Phil. Bot. **4**:1149–1152. 1911) describes 6 new species of ferns from the Philippine Islands.—S. T. DUNN (Kew Bull. 1911:362–364) has published a new genus (*Ostryoderris*) of the Leguminosae from tropical west Africa. The same author (Philip. Journ. Sci. Bot. **6**:315–317. 1911) gives a synopsis of the Philippine representatives of the genus *Milletia*, recognizing 11 species of which 3 are new to

science.—P. DUSÉN (Archiv för Botanik **10**:no. 5. 1–5. *pl. 1.* 1911) describes and illustrates a new species of *Eryngium* (*E. ombrophilum*) from Brazil.—W. R. DYKES (Gard. Chron. III. **51**:18. 1912) has published a new species of *Iris* (*I. tenuissima*) from California.—E. L. EKMAN (Archiv för Botanik **10**:no. 17. 1–43. *pls. 1–6.* 1911) under the title "Neue brasilianische Gräser" has published 19 species new to science and proposes a new genus (*Steirachne*) based on *Festuca pilosa* Nees.—A. W. EVANS (Rhodora **14**:1–18. 1912) publishes the ninth article of a series devoted to New England Hepaticae; up to the present time 169 species of this group have been recorded from the New England states.—F. W. FOXWORTHY (Philip. Journ. Sci. Bot. **6**:231–287. *pls. 34–44.* 1911) presents an article entitled "Philippine Dipterocarpaceae," recording important data concerning this family and enumerating about 40 species, of which 4 have not been described hitherto.—R. E. FRIES (Kungl. Svensk. Vetensk. Akad. Handl. **46**:no. 9. 1–72. *pls. 1–7.* 1911) presents the results of a monographic study of the genus *Petunia*, recognizing about 30 species of which 12 are new to science.—J. S. GAMBLE (Philip. Journ. Sci. Bot. **6**:289. 1911) publishes new species of *Schizostachyum* from Luzon, P.I.—J. M. GREENMAN (Ottawa Naturalist **25**:114–118. 1911) has published 4 new species and two varieties of Canadian Senecios.—A. A. HELLER (Muhlenbergia **7**:85–95. *pl. 6.* 1911) in continuation of his studies on the genus *Lupinus* records 3 new species from Oregon and California.—M. A. HOWE (Bull. Torr. Bot. Club **38**:489–514. *pls. 27–34.* 1911), in a paper on "Some marine algae of Lower California, Mexico," records 24 species of which 8 are new.—J. HUTCHINSON (Hooker's Ic. IV. **10**:*pl. 2929.* 1911) describes and illustrates a new genus (*Protomegabaria*) of the Euphorbiaceae from tropical Africa.—E. JANCZEWSKI (Bull. Acad. Sci. Cracovie 1910: pp. 67–91) has issued additional supplements to his monograph of the Grossulariaceae and includes several hitherto unpublished species and varieties from China.—P. B. KENNEDY (Muhlenbergia **7**:97–100. *pl. 6.* 109–111. *pl. 8.* 1911) describes and illustrates a new clover (*Trifolium bolivianum*) from Bolivia and a new species of *Phlox* (*P. aciculifolia*) from Nevada.—F. D. KERN (Mycologia **3**:288–290. 1911) presents a second paper on "The rusts of Guatemala"; several species are recorded, including a new *Uromyces* parasitic on *Gouania domingensis* L. The same author (Bull. N.Y. Bot. Gard. **7**:391–483. *pls. 151–161.* 1911) under the title of "A biologic and taxonomic study of the genus *Gymnosporangium*" has published the results of a monographic study, recognizing 40 species of this genus.—K. KRAUSE (Bot. Jahrb. **45**:657–660. 1911) describes 6 new species of Araceae from the Philippine Islands.—J. LUNELL (Am. Mid. Nat. **2**:142–149, 153–164. 1911–1912) has described new species and varieties of flowering plants from North Dakota, Minnesota, and Florida.—R. MAIRE (Ann. Mycol. **9**:315–325. *pl. 16.* 1911) under the title "Remarques sur quelques Hypocréacées" has established a new genus (*Nectriopsis*) based on *Sphaeria violacea* Fr.—U. MARTELLI (Leafl. Phil. Bot. **3**:1109–1132. 1911) in an article entitled "Some Philippine Pandanaceae" has published 6 new

species of *Freycinetia* and 7 of *Pandanus*.—W. A. MURRILL (Mycologia **3**:271–282. 1911) in continuation of his work on the "Agaricaceae of tropical North America" treats seven genera with rose-colored spores, to which are referred 34 species, 21 of which are characterized as new. One new generic name is proposed, namely *Volvariopsis*, which is based on *Volvaria bombycina* (Schaeff.) Quél.—G. A. NADSON and A. G. KONOKOTINE (Bull. Jard. Imp. Bot. St. Pétersb. **11**:117–142. 1911) describe and illustrate a new genus (*Guilliermondia*) of the Saccharomycetes.—J. A. NIEUWLAND (Am. Mid. Nat. **2**:129–142. 1911) under the title "Box-elders, real and so-called" proposes a new generic name (*Crula*) for several Asiatic trees, which have been regarded by most authors as congeneric with *Acer;* the first-mentioned species under the newly constituted genus is *C. cissifolia* (*Negundo cissifolium* Sieb.).—L. QUEHL (Monats. für Kakteenk. **21**:154, 155. 1911) describes and illustrates a new species of *Mamillaria* (*M. Siedeliana*) from Mexico.—H. REHM (Ann. Mycol. **9**:363–371. 1911) has published 26 new species of American and Asiatic Ascomycetes.—B. L. ROBINSON (Proc. Am. Acad. **47**:191–216. 1911) in continuation of his studies in the Compositae has published upward of 20 new species and varieties, chiefly from tropical and subtropical America. The paper also includes several new combinations with complete synonomy, as the result of careful investigations of the generic affinity of formerly misplaced species.—C. B. ROBINSON (Phil. Journ. Sci. Bot. **6**:299–314. 1911) in a second article on "Philippine Urticaceae" records 6 hitherto undescribed species of this family, and (*ibid.* 319–358) under the title "Alabastra Philippinensia" has published about 30 new species belonging to different families of flowering plants. –E. E. SHERFF (Bull. Torr. Bot. Club **38**:481–482. *pl. 26.* 1911) places on record a new variety of *Carex* (*C. lupulina* var. *albomarginata*) from Michigan.—H. SOMMERSTORFF (Oester. Bot. Zeit. **61**:361–373. *pls. 5, 6.* 1911) in a paper entitled "Ein Tiere fangender Pilz" describes and illustrates a new genus (*Zoophagus*) the affinity of which seems to be with the Saprolegniales; the fungus was discovered in Styria, Austria.—O. STAPF (Bot. Mag. *t. 8405.* 1911) describes and figures a new species of *Phyllodoce* (*P. amabilis*) from North America. The same author (Hooker Ic. IV. **10**:*t. 2927.* 1911) describes and illustrates a new genus (*Heteranthoecia*) of the Gramineae from tropical Africa.—F. STEPHANI (Sp. Hep. **4**:417–464. 1911) in continuation of his work on the Hepaticae includes in the foregoing pages 112 species of *Trullania,* 48 of which are new to science.—F. STUCKERT (Anal. Mus. Nac. Bs. As. III. **14**:1–214. *pls. 1–4.* 1911) under the title "Tercera contribución al conocimiento de las graminácees Argentinas" records 369 species of grasses of which 20 are new. The identifications and the diagnoses of new species, varieties, and forms are by the eminent specialist Professor EDUARD HACKEL.—H. and P. SYDOW (Leafl

from the Philipp

9:372–421. *pl.*

recorded several

chora) of the Dothideaceae, found on the leaves of bamboo at Kanouth, Malabar.—A. WEBER VAN BOSSE (Ann. Jard. Bot. Buitenzorg II. **9**:25–33. 1911) under the title "Notice sur quelques genres nouveau d'algues de l'Archipel Malaisien" has published the following new genera: *Bryobesia* of the Chlorophyceae, *Mesospora* of the Phaeophyceae, *Exophyllum*, *Acanthochondria*, *Oligocladus*, and *Chalicostroma* of the Florideae, and *Perinema* of uncertain relationship.—H. F. WERNHAM (Journ. Bot. **49**:346. 1911) adds another new species from Costa Rica to the genus *Hamelia* recently revised by the same author.—A. ZAHLBRUCKNER (Ann. K. K. Naturhist. Hofmus. Wien **24**:293–326. *pls. 6, 7.* 1911) in cooperation with several specialists under the title "Plantae Pentherianeae" has published a list of plants collected in South Africa by Dr. A. PENTHER; the article includes a new genus (*Pentheriella* Hoffm. & Musch.) of the Compositae.—Different authors (Kew Bull. 1911:343–348) have published several species of flowering plants new to science of which 4 are from Mexico and South America.—J. M. GREENMAN.

Alternation of generations in Delesseria.—Alternation of generations among the red algae has begun to receive much attention, and a paper by SVEDELIUS[10] is one of the latest. The material for his investigation was collected at the Kristineberg Zoological Station, Bohnslän, Sweden, during November 1910. According to the account, in this species fertilization occurs in October, early in November the spermatangia are entirely washed off, tetraspore formation occurs in November, and both tetraspores and cystocarps mature during December and January. The time of his collection, therefore, was too late for securing material for sperm-formation and fertilization, so that there is no description of the male individuals of *Delesseria*, or of the development of procarp and fertilization.

The paper begins with an account of the development of tetrasporangia; then follow tetraspore formation, vegetative nuclear divisions in the tetrasporic plants, and vegetative mitosis in the female plants. Finally there is discussed the problem of alternation of generations in the Florideae. The nucleus of the tetraspore mother cell undergoes the tetrad division, which is preceded by synapsis and diakinesis. In the diakinesis stage 20 bivalent chromosomes are present; after both heterotypic and homotypic divisions, tetraspores are produced with 20 chromosomes; the vegetative nucleus of the tetrasporic plants has 40 chromosomes; and the vegetative nucleus of the female plants has 20 chromosomes. In the resting nucleus there are present chromatin granules whose number is much higher than the double number of chromosomes. In vegetative divisions some of these chromatin granules directly unite with one another and form chromosomes, with no appearance of a spirem thread period. In the heterotypic division all chromatin granules

[10] SVEDELIUS, N., Ueber den Generationswechsel bei *Delesseria sanguinea*. Svensk. Bot. Tidskr. **5**:260–324. *pls. 2, 3. figs. 16.* 1911.

come together near a nucleolus, and then become associated into tetrads. From the number of chromosomes found in tetrasporic and female plants, and the stage at which the reduction division occurs, SVEDELIUS concludes that alternation of generations occurs in the life cycle of *Delesseria* in the sense that the reviewer proposed in his investigation of *Polysiphonia*, and that is followed by LEWIS for *Griffithsia*. SVEDELIUS denies SCHMITZ and OLTMANNS' view that the gonimoblasts of Florideae represent the sporophytic phase, comparable to those of mosses, and that the tetraspores are only the special forms of reproductive cells, comparable to brood cells or "Nebenfruchtformen," and with no fixed place in the life-history.

In closing, he proposes to drop out the term "carpospores," and to substitute "carpogonidia," the reason being that the spore has the haploid number of chromosomes and represents the gametophytic phase, whereas the carpospore has the diploid number and represents only a stage in a prolonged phase of the sporophyte.—S. YAMANOUCHI.

Plant proteins.—ZALESKI[11] is making a study of the transformation of food materials in ripening seeds. The present paper deals only with the nitrogenous materials in their relation to the synthesis of proteins. By applying a method used in 1905, he finds that various non-protein organic N-containing materials are transformed to proteins during ripening. The method consisted in removing green peas from the pod and coats to avoid additions from other portions, and in making determinations of the N in proteins, in amino acids, and in organic bases. The determinations for one portion was made immediately after the removal, and for other portions 2–5 days later. In all cases considerable amounts of amino acids and organic bases were transformed to proteins. A typical analysis follows:

	Control	After 5 days storage
N of protein	79.2 per cent of total N	89.2 per cent of total N
N of amino acids	8.7	4.6
N of organic bases	10.8	5.6
N of other compounds (difference)	1.4	0.8

Under similar treatment, *Zea mais* showed little protein synthesis, and the sunflower only protein decomposition. In the pea the synthesis was less than half as fast in the absence of O_2 as in its presence. Drying of the seeds also greatly hastened the synthesis.

ZALESKI brings together the evidence for the conception that the amino acids resulting from the hydrolysis of a plant protein are the ones involved in its synthesis. He considers the two processes as two phases of a reversible

[11] ZALESKI, W., Zur Kenntnis der Stoffwechelselsprozesse in reifenden Samen. Beih. Bot. Centralbl. **27**:63–82. 1911.

reaction. This accords with the evidence on the animal side, and stands in opposition to WASSILIEFF'S view that asparagin is the immediate material from which plant proteins are synthesized, and to the PFEFFER view that proteins may be synthesized by the installation of NH_3 into organic compounds without the amino acids as intermediate forms. ZALESKI raises the question whether the same enzymes cause both the condensation and hydrolysis. Both protease and rennin were found in the ripening seeds, but no tests were run for ereptase. The hydrolytic activity diminished as ripening progressed, due either to the destruction of the enzyme or to its transformation to an inactive form, for no evidence for an anti-enzyme could be found.—WILLIAM CROCKER.

Potassium in plants.—WEEVERS[12] has made a rather extensive study of the distribution of potassium in plants. He used, in the main, MACCALLUM'S method of treating the tissues with sodium cobalt nitrite, followed, after thorough washing with water, by ammonium sulphide. He finds potassium in all plants except Cyanophyceae. The nucleus and chloroplast are always potassium-free, while the vacuole is rich in it, and the cytoplasm contains considerable. The writer believes, contrary to MACCALLUM, that these reagents are not capable of showing the localization of the potassium in the cell. The apparent localization found by the latter worker was probably largely due to precipitation determining the concentration gradients in both the reagent and the potassium salt. Essentially all the potassium found in the plant cell can be dissolved out of the dead cell with either water or 50 per cent alcohol, so the author believes the element exists in the form of inorganic salts and not as a part of the protoplasmic organic constituents. The pollen grains of *Tulipa* and *Crocus* are potassium-free, and will develop normal tubes in a potassium-free medium. In these cases then, among the higher plants, potassium is not necessary for growth. The absence of potassium in the chloroplasts is offered as fatal to the assumption of various workers that it plays an important rôle in photosynthesis. The author believes that his findings agree with the view that potassium in the growing point is connected with protoplasm construction, while in the vacuole it aids in the production of osmotic pressure. The facts reported in this work, agreeing in the main with those reported by MACCALLUM, show how little we know about the physiological rôle of potassium.—WILLIAM CROCKER.

Development of Laminaria.—The development of the Laminariaceae from spore to adult has been very little studied. YENDO[13] has studied the development of three forms, *Costaria Turneria*, *Undaria pinnatifida*, and *Laminaria* sp., and the results may be summarized as follows: The sporelings

[12] WEEVERS, TH., Untersuchungen über die Lokalization und Funktion des Kalium in der Pflanzen. Recueil des Travaux Bot. Néerl. **8**:289–332. *figs.* 3. 1911.

[13] YENDO, K., The development of *Costaria*, *Undaria*, and *Laminaria*. Ann. Botany **25**:691–715. *pls.* 53–55. 1911.

develop first as confervoid bodies, growing by a single apical cell. This body then becomes monostromatic, with a monosiphonous stipe. The two cells situated side by side at the same level below the apical cell initiate the monostromatic blade, and this blade becomes distromatic at base, and at the same time the monosiphonous stipe becomes polysiphonous. A new meristematic tissue appears at the transition region between blade and stipe. The growth both in length and breadth is due to the apical and stipo-frondal growth up to a certain period. The apical growth gradually diminishes and finally ceases, and then erosion of the apex of the blade follows. A single precortical layer of large parenchymatous cells is developed at the transition region between the already existing two layers. The hyphal cells are formed as the precortical layer becomes doubled, and the expansion of their distal ends into a trumpet shape takes place at the intercellular spaces. The ribs and meridional region are formed by special thickening of the cortical layers. The dorsiventrality of the lamina, if it exists, is indicated simultaneously with the formation of these parts. The cryptostomata in the Laminariaceae do not originate from a single cell.—S. YAMANOUCHI.

Geotropism.—ÁRPÁD PAÁL[14] finds that reduction of the air pressure lengthens the geotropic reaction and presentation times in the root of *Phaseolus vulgaris*. The presentation time was 6 minutes at one atmosphere; 20 minutes at 0.74; 35 minutes at 0.21; and 70 minutes at 0.08. The reaction time was found markedly variable when all controllable conditions were constant. From the average of many measurements, the author finds that if at one atmosphere the reaction time is considered as 1, at 0.74 atmosphere it is 1.09; at 0.34 atmosphere 1.39; at 0.21 atmosphere 1.60; and at 0.08 atmosphere 2.20. It is interesting to see what slight reductions in pressure cause a lengthening of these critical times. It is well known that the respiratory intensity is not cut until the pressure is reduced to a much greater degree. If the effects here are due to the reduced oxygen pressure, as is assumed, one sees what a complex rôle oxygen plays in the organism, the several functions apparently having very different critical pressures. The author concludes that the lengthening of the reaction time is due to the sum of the effect of reduced pressure upon the sensory and motor phases and to the telescoping of these phases.—WILLIAM CROCKER.

Formaldehyde and green plants.—GRAFE[15] finds etiolated plants or non-chlorophyll parts of green plants very sensitive to vapors of formaldehyde, especially if the cultures are illuminated. The chlorophyll-bearing parts (*Phaseolus vulgaris*) are not injured by concentrations as great as 1.3 per cent

[14] PAÁL, ÁRPÁD, Analyse des geotropischen Reizvorgangs mittels Luftverdünnung. Jahrb. Wiss. Bot. **50**:1–20. 1911.

[15] GRAFE, VIKTOR, Untersuchungen über das Verhalten grüner Pflanzen zu Gasformigen Formaldehyde. Ber. Deutsch. Bot. Gesells. **29**:19–26. 1911.

of the atmosphere. Illuminated cultures of green seedlings in CO_2 free chambers gave much greater growth and increased dry weight if formaldehyde vapors were present than if they were not. It was necessary of course to protect the non-chlorophyll-bearing parts from contact with the vapors. Formaldehyde increases the reducing sugars in *Phaseolus* at the expense of starch deposit. This may account for the failure of starch to appear as a result of the synthesis of formaldehyde. These results, with the more telling experiments of SCHRYVER,[16] USHER and PRIESTLY,[17] and others, furnish strong evidence that formaldehyde is an intermediate product in photosynthesis.—WILLIAM CROCKER.

Phosphorus content of oat grains.—LEWONIEWSKA [18] finds that the phosphoric acid content of oat grains, measured both in absolute amount and in its ratio to the nitrogen, varies greatly with cultural conditions, involving variation in fertilizers and nature of the soil. The variation is mainly due to the inorganic and phytin phosphoric acid, and not to the protein and lecithin phosphoric acid. The author thinks that an excess in the soil leads to its storage in the inorganic and phytin forms. A variation in the nitrogen content of the grain is mainly due to the protein nitrogen. The author concludes that the phosphoric acid supply in the soil can be best judged by the ratio of inorganic and phytin phosphoric acid to protein nitrogen in the grain. The probabilities are that the conditions determining the proportion of absorption and form of storage of nitrogen and phosphorus compounds are much more complex than the author assumes.—WILLIAM CROCKER.

A new genus of yeasts.—NADSON and KONOKOTINE[19] have described a new genus (*Guilliermondia*) of Saccharomycetes, in the culture of which they observed the pairing and fusing of unequal cells ("gametes"), resulting in a cell that became an "ascus" producing one spore (sometimes two spores). In the germination of the spore under usual conditions, cells with the ordinary budding habit were produced. The full account is in Russian and the brief summary in French.—J. M. C.

---

[16] SCHRYVER, S. B., Photochemical formation of formaldehyde in green plants. Proc. Roy. Soc. London B **82**:226–232. 1910; rev. in BOT. GAZ. **51**:470–471. 1911.

[17] USHER, F. S., and PRIESTLY, J. H., Proc. Roy. Soc. London B **84**:101–112. 1911.

[18] LEWONIEWSKA, S., Schwankungen in dem Gehalte der Pflanzensamen an einzelnen Phosphorsäureverbindungen in ihrer Abhängigkeit von Vegetationsbedingungen. Bull. Acad. Sci. Cracovie 1911:85–96.

[19] NADSON, G. A., and KONOKOTINE, A. G., *Guilliermondia*, un nouveau genre de la famille des Saccharomycètes à copulation hétérogamique. Bull. Jard. Imp. Bot. St. Pétersbourg **11**:117–143. *figs. 45*. 1911.

VOLUME LIII NUMBER 5

THE

BOTANICAL GAZETTE

MAY 1912

RELATIONS OF PARASITIC FUNGI TO THEIR HOST PLANTS

I. STUDIES OF PARASITIZED LEAF TISSUE

ERNEST SHAW REYNOLDS

(WITH NINE FIGURES)

Various phases of pathologic study have occupied the attention of botanists at different times. Before the exciting causes of diseases in plants were known, the general external appearance of the affected organ was described. Later, most of the attention was directed toward the discovery of the parasitic organisms which cause the derangements, and incidentally the study of the physiologic responses of the host was begun. Within the last few years many students of the subject have examined various morphologic changes which occur in diseased plants, first dealing almost entirely with the gross anatomic appearance, but later making more minute histologic and cytologic investigations. Leaf tissue, when invaded by fungi, however, has not been thus carefully studied. Moreover, comparative studies are always helpful in deciding general principles, and so it is in pathologic morphology. Only as we become acquainted with many examples of cytologic and histologic changes, shall we be able to approximate the truth regarding the reaction of the host plant to parasitic invasion. The practical value of such results can hardly be doubted. WOODS (92) has written of this matter as follows:

To most successfully combat a disease, we should know the causes that contribute to it, and as much about the causes as possible. We should under-

stand the pathological reactions of the diseased plant. Only in this way shall we be able to remove the causes or protect the plant against them or assist it to recover.

If, then, we desire to find a safe remedy, we must know all that is possible to know concerning the disease. As a link in the chain of evidence this paper is presented, with the hope that it may serve to extend knowledge of the reaction of leaf tissue to fungous invasion.

Historic

The relations between parasitic fungi and their host plants are of various kinds. The subject might be divided into two parts: (1) the changes in the fungi when grown upon various substrata, and (2) the effects of the fungus upon its host plants. Among the latter we can easily distinguish two classes, though one class is dependent upon the other; those changes which are disturbances of the physiologic processes, and those which are changes in the morphologic structure.

As we are to deal with the latter class in this paper, we shall turn our attention to the investigations on pathologic morphology which have previously been reported. The two phases which we must consider are (1) the anatomic and histologic, dealing with abnormal organs and tissues, and (2) the cytologic, dealing with abnormal cell structures.

Various pathologic modifications of the floral organs have been noted. MOLLIARD (**48**) described various changes in flowers caused by *Peronospora*, *Cystopus*, and other fungi, as well as by insects. WAKKER (**84**), in his most useful paper, reported additionally a number of abnormalities in some or all the organs of various flowers. The reproductive organs and corolla of two species of *Teucrium* are attacked and changed in structure by the larvae of *Copium* (HOUARD **29, 32**). Galls on the flowering parts of *Euphorbia Cyparissias* also were described by HOUARD (**30, 31**). The changes which WARD (**86**) cited as occurring in the buds of *Lilium candidum* are less striking but none the less interesting. The effects of *Cystopus candidus* upon the various organs of its host as described by EBERHARDT (**19, 20**) are notable.

TREUB (79) described the effect of *Heterodera* upon the root structure, and other writers have also studied abnormal root structures.

Stems and branches are also subject to invasion by parasites of various kinds. A somewhat detailed description of the deformation caused by *Ustilago* in the stem of *Zea Mays* was given by Miss KNOWLES (35), while WAKKER (84) showed that many groups of fungi have the power of changing the appearance and structure of stems. The Exoasceae cause numerous hypertrophies and other abnormalities in the vegetative organs as shown by SMITH (70). HARTMAN (27) described the witch broom of the white fir. Several of our common flowering plants, such as *Hepatica* and certain species of *Euphorbia*, were described by MEEHAN (43) as having elongated petioles and stems when attacked by rusts. EBERHARDT (19, 20) gave some histologic data regarding various stem tissues in pathologic condition. Some abnormal anatomic conditions were described by MOLLIARD (50).

The effects of disease upon the forms of leaves are among the most noticeable of the pathologic phenomena. WORONIN (93*a*) found various modifications of the leaf tissue caused by *Exobasidium Vaccinii*. *Exoascus* also causes very striking abnormalities in the leaves of various species of *Prunus* that have been described by Miss KNOWLES (34), ATKINSON (4), and SMITH (70). WAKKER (84) described various leaf modifications due to fungi. Some histologic changes of the needles of the witch broom of the white fir were noted by HARTMAN (27). The observations of PEGLION (63) showed that other kinds of rusts cause changes in the structure of leaves and stems. The anatomic changes caused by species of *Gymnosporangium* were described by WÖRNLE (94*a*); and ANDERSON (1) described the same for *Aecidium elatinum* on *Abies balsamea*. Plants growing normally in one range of temperature, when placed in a colder climate are often noticeably affected. BONNIER (6, 7), WAGNER (83), and HOUARD (28) have given us valuable results in their studies on this subject. Intumescences caused by abnormal environment have been described by Miss DALE (13, 14, 15), VON SCHRENK (67*a*), and others. The effects of various chemical substances upon plants have been studied. Of the work on this

subject we may mention that of WILFARTH and WIMMER (89, 90). CROCKER and KNIGHT (12), NĚMEC (59), and ANDREWS (3). Finally, we may note that wind has been found to play an important part in the production of abnormalities. Such observations were made by HANSEN (26a) and BRUCK (9). The general subject of "pathological plant anatomy" has been most satisfactorily reviewed by KÜSTER (38), who has also published various articles upon various phases of the subject, but especially concerning the anatomic features of gall tissues (37). This review of papers upon the subject of the histologic and gross anatomic changes, though incomplete, will serve to show the present extent of the subject, and through these references the rest of the papers may be traced.

From the following review of work upon pathologic cytology it will be seen that fungi, insects, poisonous substances, changes of temperature, and other physical forces all tend to modify the plant cell.

WORONIN (93a) found that *Exobasidium Vaccinii* on *Vaccinium Vitis-Idaea* reduces the amount of chlorophyll, and that the red-colored erythrophyll takes its place in the palisade cells. Miss KNOWLES (34) found that when peach leaves are attacked by *Exoascus deformans* the epidermal cells become rounded and have thickened walls, the palisade cells become nearly isodiametric, and the protoplasm is reduced in amount. ATKINSON (4) found that certain of the parenchyma cells become "very much elongated and curved or sinuous in form." TUBEUF (80) mentioned secondary cell formation in the palisade of *Populus niger* in leaves attacked by *Exoascus aureus*. In the cells of *Lilium candidum* affected by a *Botrytis* disease, WARD (86) found that the mycelium causes a swelling, dissolving, and discoloring of the cellulose cell walls, but does not directly affect the protoplasmic parts. The same observer (87) described similar effects of a *Botrytis* disease upon the snowdrop. In WAKKER'S paper (84) there are occasional references to cytologic phenomena. In most of the hypertrophied parts no chlorophyll is formed. Calcium oxalate is in the form of masses of small crystals ("Drusen") in the flower and leaf cells of *Rhamnus Frangula*, but is wanting usually in the parts attacked by *Aecidium*. In other cases numerous small individual crystals

are formed. Starch is often abundant in certain hypertrophies. Bacteria were reported by DANGEARD (16, 17) as causing the swelling of the nucleus of *Euglena*, the disappearance of the nucleolus, and the disorganization of the chloroplasts. The effect on the contents of cells in the process of fermentation has been studied by MATRUCHOT and MOLLIARD (46), and PEIRCE (64*a*) has described the changes in the root tubercles on the bur clover. *Cystopus candidus* usually causes an unusual deposition of starch and formation of chlorophyll in parts usually free from these substances, as described by EBERHARDT (19, 20). Other students, as GRANT SMITH (69), NORDHAUSEN (61), W. G. SMITH (70), WÖRNLE (94*a*), HALSTED (25*b*), MIYOSHI (44*b*), and HARTIG (26*b*), have noted the effects of fungous invasion upon the cellulose walls, and the distribution of starch and of calcium oxalate. The cellulose walls may be thickened or dissolved, and the starch and calcium oxalate content may be increased or decreased as determined by the season, the specific invader, and the host. WARD (88) has found that in the wheat plant the hyphae of the invading rust do not seem to affect the "chlorophyll-corpuscles or the nuclei until a late stage of growth." The leaves of the witch broom of the white fir are described by HARTMAN (27) as having small amounts of chlorophyll and starch. WÖRNLE (94*a*) reports that *Gymnosporangium* causes excessive nuclear division and cell formation in pine needles. The Ustilagineae, according to STROHMEYER (75), cause various changes in the cells of the host, both hypertrophy and hyperplasy of the parenchyma occurring. MOLLIARD (48) described a number of cytologic changes caused by insects and fungi growing on various hosts. *Cystopus candidus* causes the cells to assume abnormal forms and sizes, the nuclei to enlarge, and the normal chlorophyll content to change. *Peronospora* does not affect its hosts in this way. *Puccinia Violae* on *Viola silvestris* causes the nuclei and the nucleoli to enlarge, and the power of division of the former to increase. The petals of *Euphorbia Cyparissias* when attacked by *Uromyces scutellatus* and *U. praeminens* show cells with enlarged nuclei and chlorophyll formation.

The effects of various insect parasites upon the vegetative cells may be summed up in general thus: nuclei and nucleoli

enlarged, chloroplasts reduced in size, often a more abundant protoplasm than normally, and variations in the calcium oxalate content. In some fungous galls GUTTENBERG (24) found a tendency for the nucleus to become lobed, to divide amitotically, to decrease in size, and to force the chromatin toward the periphery. The cytologic features of some gall tissues, resulting from insect invasion, has also been described by MOLLIARD (49). The nuclei show a decided tendency toward amitotic division, which often results in the presence of several nuclei in a cell, with no formation of new walls. The nucleoli as well as the nuclei become greatly hypertrophied, and the former may be divided often without the subsequent division of the nucleus. At times the nucleus multiplies by a method of budding in addition to the more common means of abstriction. The nuclear membrane may finally disappear, and eventually even the nucleoli may become disintegrated. HOUARD (29) reported similar hypertrophy of the cell organs of the flowers of *Teucrium* when attacked by the larvae of *Copium*. PERCIVAL (64*b*) described the effect of *Synchytrium* in the potato "wart disease" upon the host cells. These enlarge, the cytoplasm increases, and the nucleus becomes deformed. "The organisms stimulate the invaded cells and at the same time appear to stimulate division and growth in the adjoining cells." Changes in root cells have been noted from time to time, especially in the studies on mycorhizae. MAGNUS (41) found the nucleus modified in these symbiotic structures. SHIBATA (68) notes that the nuclei in such conditions become enlarged, amoeboid, and divide amitotically. They may be strongly colored at first, but later they seem to become normal as regards division and color. ZACH (94*b*) describes the following cytological changes in cycad root cells due to fungous invasion. The nucleus becomes amoeboid or otherwise misshapen, the starch is dissolved away, the calcium oxalate increases in amount, and finally nucleus and plasm die. The cells of the growing point and the *Anabaena* region are not seriously invaded. MOLLIARD (52) reported that the nematode worm lives in a tissue which has giant cells with numerous nuclei and enlarged nucleoli. VUILLEMIN and LEGRAIN (82) reported various nuclear phenomena caused by the same worm in symbiotic relationship with the roots

of plants cultivated in the dry Sahara region. MOLLIARD (51) found "nuclear protoplasmic division" in stems attacked by *Phytoptus*. NAWASCHIN (54) described strongly hypertrophied cells, and enlarged nuclei with poor chromatin content, in tissues invaded by *Plasmodiophora Brassicae*. TOUMEY (77) noted that the nucleus of a crown-gall cell becomes much enlarged and finally "appears as if eroded on the surface." The nucleoli are very persistent. Under abnormal conditions the root tip of *Allium Cepa* shows enlarged cells and nuclei (some lacking nucleoli), and often an increased amount of chromatin. NĚMEC (56) also noticed nuclear fragmentation in the same root tips. The nuclei in leguminous root tubercles are reported by PARATONE (62) as becoming amoeboid and abnormally colored; CHODAT (11), however, noted no great changes.

The effects of changes of temperature upon cell structure have also been studied to some extent. PRILLIEUX (65) grew seedlings in heated soil, and found that the nuclei became numerous and variable in form. They increased by fragmentation and often possess numerous nucleoli of various shapes and sizes. These are vacuolated. NĚMEC (57) found that nuclei assume amoeboid forms in lowered temperatures. SCHRAMMEN (66) found that abnormal nuclear division ("pseudomitosis"), abnormal size of nucleus, and abnormal mass of nucleolin and kinoplasm resulted from changing the temperature surrounding the growing point of a *Vicia Faba* stem. MATRUCHOT and MOLLIARD (45, 47) give very detailed descriptions of abnormal nuclei produced at freezing temperatures, especially noting the distribution of chromatin. NĚMEC (58*a*) produced multinucleated cells in the roots of *Vicia Faba* by placing them in a 1 per cent copper sulphate solution; upon returning them to normal conditions karyogamy took place and uninucleated cells were formed. GRANT (23) has reported upon various multinucleated cells. ANDREWS (2) found that a nucleus, deprived of its nucleolus can survive for a long time, but a new nucleolus is not formed. The influence of benzene gas upon cell formation was studied by BLAZEK (5*a*), who reported that simultaneous nuclear division takes place, and many daughter nuclei are formed either with or without subsequent cell wall

formation. WASIELEWSKI (85) and WISSELINGH (91) have discussed the question of amitosis in various tissues. Miss DALE (13, 15) found that in certain intumescences caused by abnormal light, heat, etc., oil is formed in place of starch, the nuclei become club-shaped and highly refractive, and the nucleoli are often increased in number. Amitosis was found to be almost universal, and formed nuclei of unequal size. VON SCHRENK (67*a*) described similar intumescences due to chemic stimulation. Other studies upon the structure of intumescences were made by SORAUER (71, 72) and STEINER (73). The structure and the pathologic modifications of chromatophores have been studied by KÜSTER (39) in *Ceramium* cells, where under various influences they may be contracted into drops or flattened out into irregular bands. NĚMEC (55) has reported the decrease in the number of chromosomes in old tissue, and their increase in hypertrophied cells. Besides these already enumerated, it would be well to note the following as articles dealing with several phases of the subject, and containing valuable lists of references: ZIMMERMAN (96, 97), WARD (87), UNGER (81), FAIRCHILD (21), and NĚMEC (60). Some abnormal nuclear phenomena have been described also by MIEHE (44*a*) near wound tissue, KOHL (36) in cells under the influence of asparagin, and ZACHARIAS (95) under various influences.

Summing up the results so far obtained in the study of the effects of parasitic invasion and abnormal physiologic influence upon the histologic and cytologic elements of plants, we find that the various kinds of tissues, collenchyma, parenchyma, sclerenchyma, and cork, may be abnormally developed or repressed; cell walls may be simply perforated, or much thickened and more or less changed in constitution; secondary cell formation may arise; nuclei and nucleoli may be increased or reduced in number and size, and variously deformed; chromatin may likewise be increased or decreased; the cell sap may acquire a new color; the starch and calcium oxalate content may change; and the chromatophores changed in appearance and efficiency.

Methods

For the investigations to be reported here the ordinary methods of preserving the material were used. The medium solution of

chromacetic acid was found to be the most useful killing and fixing fluid experimented with. Picric alcohol was less satisfactory, because stains of several kinds refuse to affect the tissue when preserved in this solution. For the same reason, picronigrosin was not very successful. An abundance of material was usually kept in the dry condition as herbarium specimens, and some was preserved as well in 4 per cent formalin. Paraffin, melting at about 52° C., was used for most of the work, though the harder grade, melting at 60°, was employed for some of the tough, resistant leaf tissues.

The orseillin-anilin blue method of staining, as outlined by STRASBURGER (74a), was used for all of the preliminary work. This combination serves to differentiate the fungus in the host tissue, and also to make it easy to distinguish the cell contents. The latter stains rather darkly with orseillin, and the host cell walls lightly with the anilin blue. The fungous walls stain much more deeply with the anilin blue. Later in the work, when studying the nucleus, Haidenhain's hematoxylin was used, about as outlined by CHAMBERLAIN (10). The differentiation thus obtained was very satisfactory, since the nucleus held the stain more tenaciously than did the cell walls. Fuchsin also was used to some extent.

About 50 different specimens were preserved, sectioned, and examined. Many of these failed to be of value, either because of the great destruction of the host tissue by the fungus, or because of the absence of distinctive and recognizable cytologic changes. The drawings were all made with a camera lucida; and a $\frac{1}{12}$-inch, achromatic oil immersion objective was used for all high magnifications in all camera drawings. The drawings, with one or two exceptions, are of the same magnification, and hence can be compared directly with one another. The attempt was made to get satisfactory material which would illustrate as great a diversity of host plants as well as of fungi as possible. In the following pages, therefore, there will be representatives of both monocotyledons and dicotyledons, and of the latter from several diverse families. The Uredineae, the Ustilagineae, the Phycomycetes, and the Fungi Imperfecti are all represented. The descriptions

of normal and diseased material are from the slides prepared by the methods above mentioned. The normal tissue was cut from the same leaf as the diseased, unless the leaf showed in all parts the effect of the parasitism. In this case a leaf close to the diseased one was chosen in order to have comparable material.

Observations

1. Gaylussacia baccata (Wang.) C. Koch.—The cause of the disease is not clear. The diseased area is blackest on the upper side, and a white deposit is found on the lower surface of the leaf. The normal leaf tissue is as follows: (1) a single layer of nearly isodiametric cells in the upper epidermis; (2) a single layer of palisade cells; (3) a rather loose, spongy parenchyma with comparatively large intercellular spaces; and (4) a lower epidermis of cells usually somewhat smaller than those of the upper epidermis. The plant studied was collected in early summer, and hence the leaves were fully formed, but still in a vigorous condition. The location of the plant was at the edge of a wooded area, but open, so that the leaves received an abundance of light. The leaf cells have a thin peripheral lining of protoplasm, in which the chloroplasts and the nuclei are imbedded. The cuticle is nearly colorless, and much thicker over the upper than over the lower epidermal cells.

The parasitized leaf shows a number of changes. Just before the palisade cells and after the sponge cells begin to collapse, they are filled with a uniformly brown-stained material. Previous to this they are filled with a granular mass which is stained yellow-brown. In both of these stages of degeneration there are neither chloroplasts nor nuclei to be seen. At the same time, the upper epidermal cells become considerably elongated, and the cuticle is light yellow to brown. In the last phase of degeneration the epidermal cells become completely collapsed, the palisade cells are much shrunken, and the sponge cells have practically disappeared, while the cell walls are uniformly brown, and the cells empty.

2. Viola cucullata Ait. (?), parasitized by *Puccinia Violae* (Schum.) DC.—The normal leaf tissue of this plant is rather poorly differentiated. The epidermal cells are very irregular in shape and size, and the cuticle is thin. The mesophyll is composed of a loose

mesh of rounded cells, stretching from one epidermis to the other. The tissue is evidently very easily ruptured, and is seldom complete except at the veins and in connection with the fungous spore beds. The plants examined were growing in a well-shaded and damp location, and were collected in early summer.

In the parasitized regions the cells are closely compacted, and more or less bound together by the invading mycelium which fills the intercellular spaces. Here also the hematoxylin stains much more intensely than in the normal tissue. There seems to be some hyperplasy of the mesophyll. The epidermis is ruptured by the

FIGS. 1–3.—Cells from leaf of *Viola cucullata* parasitized by *Puccinia Violae*: fig. 1, two cells showing deformed nuclei and increased number of nucleoli; fig. 2, cell showing three nuclei and a few chloroplasts; fig. 3, cell showing three deformed nuclei.

spore bed, but the influence of the fungus does not extend far beyond this radius. The nuclei, which are not prominent in the normal cells, become somewhat enlarged, and increase in number in the cells. There are numerous instances where the number is increased to two, while some cells were noticed that contained three nuclei. The nuclei are also more or less deformed, varying from nearly circular in cross-section to oval, oblong, or slightly pear-shaped. The chloroplasts seem to be little affected, at least in shape and size, by the presence of the parasite. Fig. 1 shows some examples of the deformations to the nuclei which are found in the cells near the

spore bed of the rust; fig. 2 shows the abnormal number of three nuclei in one cell; while fig. 3 shows some deformation accompanying the hyperplastic condition.

3. PSEDERA TRICUSPIDATA (Sieb. and Zucc.) Rehder, parasitized by *Phyllosticta Labruscae* Thum.—The normal leaf tissue is similar to that of the *Gaylussacia* described above, and the pathologic changes are very much alike in the two plants. The browning and collapse of the epidermal, palisade, and sponge cells are common to both. The early disappearance of nuclei and chloroplasts is also similar in the two. There is in this case a granular protoplasm in the cells next to the dead area, while the homogeneous brown mass is not formed. The sponge tissue is more completely disorganized than the palisade. This plant, collected in early July, was growing upon a wall exposed to the morning sun.

4. SMILAX GLAUCA Walt., parasitized by a member of the Phaeodidymae of the Sphaerioidaceae.—The leaf parenchyma is not differentiated into palisade and sponge tissues. The diseased area is badly shrunken and broken down. The fungous perithecia are scattered irregularly over this dead area. Because of the thorough killing of the host tissue, no special cytologic changes could be noted. At the edges of the diseased area the cells of both the upper and lower epidermis are turned brown to black, while some of the mesophyll cells are filled with a uniformly brown-staining material. The intercellular spaces and the primary lamellae are often stained very deeply by the hematoxylin. In this transition region no cell organs are visible, and whatever is left of the protoplast is turned black or brown. This coloration sometimes extends to the cell walls as well.

5. POTENTILLA CANADENSIS L., parasitized by *Puccinia Potentillae* Schw. (?).—There is a double parasitism represented here. *Darluca filum* was found growing abundantly upon the spore beds of the rust, and at times apparently directly upon the leaf tissue of *Potentilla*. This latter condition, however, may have been due to the rust mycelium in the tissues which had not yet produced a noticeable spore bed.

The normal structure of this *Potentilla* leaf is somewhat more complex than that of the *Viola* described previously. The palisade

cells have a more oblong longitudinal section than the sponge cells and are more closely packed. The plants collected were growing in a place which was shaded all of the afternoon and part of the morning. The collection was made about the middle of July.

When the leaf is attacked by the rust, the epidermis is broken, the palisade is poorly developed, and more or less replaced by rounded cells common to the sponge and the diseased palisade tissues. In the early stages of the disease the epidermis separates from the mesophyll. There is some hyperplasy of the sponge tissue. The cells, which remain in the tissue directly under the spore beds, are widely scattered and separated by the mycelium of the rust. When the rust is parasitized by *Darluca* the palisade tissue is less abnormal and disorganized. The chlorophyll seems to have largely disappeared from the cells which are within the influence of the rust. A similar effect upon the nuclei is usually seen. An increase in the number of nuclei in individual cells was noticed, however, in tissue just below a perithecium of *Darluca*, which was found imbedded directly in the tissue of the *Potentilla* leaf. Fig. 4 shows two contiguous cells, each having two nuclei; there is also a distinct deformation of these double nuclei.

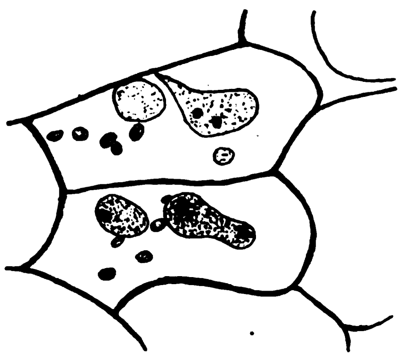
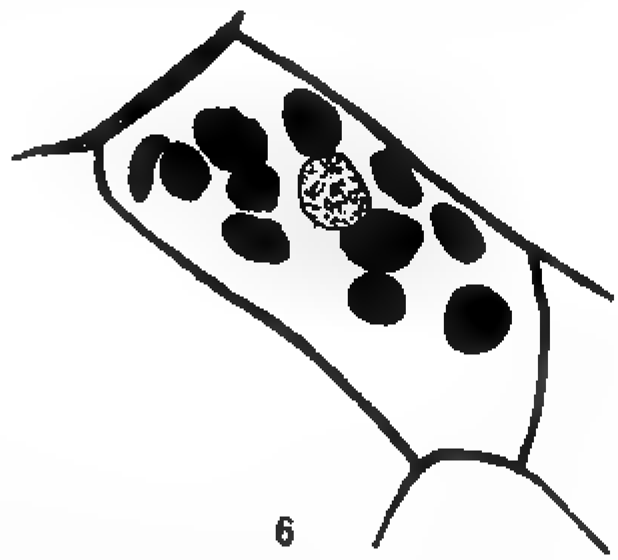


FIG. 4.—Two cells from *Potentilla canadensis* leaf parasitized by *Puccinia Potentillae*, showing two nuclei in each, and in one a suggestion of the beginning of an abnormal division of one of the nuclei.

6. PANICUM LATIFOLIUM L.—The cause of the disease upon this *Panicum* is not clear, though it is surely of fungous nature. The normal leaf tissue is that of the ordinary grasses. The epidermal cells on both sides of the leaf are very large as compared with the simple mesophyll cells which occupy the space between the two layers of epidermis. In the healthy chlorophyllose cells there is only a thin peripheral lining of protoplasm in which the nuclei and the chloroplasts are distributed.

Many of the cells of the diseased area are filled with a homogeneous substance which stains blue, so that at a glance the location of the diseased tissue can easily be discovered. The protoplasm, which is somewhat more abundant and more evenly distributed in the diseased cells than in the normal, is very finely granulated. Many of the diseased cells show two nuclei. All of the nuclei in the vicinity stain deeper or retain the stain more tenaciously than in the healthy tissue, and are relatively larger than in the normal cells. The chlorophyll has largely disappeared from the cells close to the point of invasion, but farther away the



6

FIGS. 5, 6.—Cells from leaf of *Panicum latifolium:* fig. 5, cell from a diseased leaf, showing an enlarged nucleus and diminutive chloroplasts; the cell is slightly plasmolyzed; fig. 6, cell from an unaffected region, showing a normal nucleus and normally sized chloroplasts.

chloroplasts are merely reduced in size. Figs. 5 and 6 show enlarged and normal nuclei respectively; the difference in the size of the chloroplasts is easily seen also.

7. PYRUS MALUS L., parasitized by *Gymnosporangium* sp.—The structure of this leaf is somewhat more complex than any of those previously described. The upper and lower epidermal cells are in single layers, and are partly isodiametric and partly oblong in shape. The palisade cells, which are in two layers, have their nuclei symmetrically placed in the peripheral protoplasm close to the middle of the lateral walls. The chloroplasts are also arranged along the same walls. The cells of the upper palisade layer are about a third longer than those of the second layer, and are about the

same width as those cells. This palisade occupies half the thickness of the leaf. The sponge cells are loosely connected and have large air chambers scattered among them. The tree, from which the diseased leaves were taken, was growing in a thicket, and about 50 feet from a *Juniperus* tree.

The portion of the leaf which is parasitized is about twice as thick as the normal tissue. This thickening is due to two factors, the hypertrophy of the sponge tissue, and the presence of masses of mycelium. The palisade cells are least affected. The cells in the upper layer are shortened until they are about the length of the cells in the second layer. The space thus left between the upper epidermis and the palisade cells is occupied by mycelium from which the pycnia are developed. The upper epidermis is puffed up and ruptured, the cells are nearly collapsed, the walls are changed to a brown color, and the cuticle is mostly destroyed. The parenchyma cell walls seem to remain about normal. The sponge cells are enlarged to twice or thrice their normal diameters, and the spaces between are filled with the heavily stained mycelium. The nuclei of the sponge cells are the first to show the effects of the presence of the fungus by becoming rather larger than they are normally. They are not, however, otherwise materially changed. Many cells are partially filled with a yellow, granular deposit (fig. 7).[1]

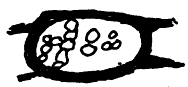


FIG. 7.—A diseased cell from a leaf of *Pyrus Malus* parasitized by *Gymnosporangium*, showing no contents except irregular yellowish granules.

8. SMILACINA RACEMOSA (L.) Desf., parasitized by *Phyllosticta cruenta* (Fr.) Kicks.—The leaf of *Smilacina* is rather simple in structure. The upper epidermis has relatively large oblong cells, interspersed at intervals with short cubical cells. The lower epidermis has smaller and usually more regular cells. Between these two layers is a rather loose parenchyma with large air spaces, and with the larger number of cells close to the upper epidermis. The plants collected were growing at the side of a road through the woods, where the light was rather weak and there was abundant moisture.

[1] Fig. 7 was drawn with a ⅛-inch objective, and hence is not on the same scale as the other figures.

In the diseased area the cuticle and the epidermal cells are affected to a greater distance from the center of infection than the sponge cells. They are early turned brown and the epidermis is shrunken. The sponge tissue is badly disorganized, but chloroplasts and nuclei are present. The latter attain a larger size, and have a light brown color, whereas when normal they are easily stained with hematoxylin. They often have two nuclei and a granular plasm. Later, in the degeneration of the nucleus, the nucleoli disappear and the nucleus stains deeper. The chloroplasts may later disappear and afterward the other constituents of the cell. Fig. 8 shows the light brown enlarged nuclei in cells affected by the parasite.

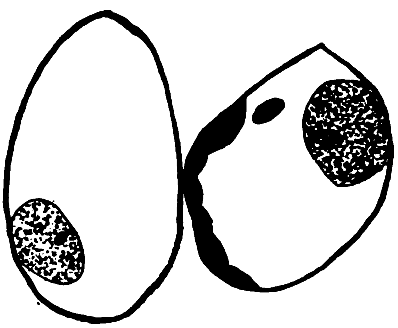


FIG. 8.—Two cells from a leaf of *Smilacina racemosa* parasitized by *Phyllosticta cruenta*, showing enlarged nuclei.

9. CASTANEA DENTATA (Marsh.) Borkh., parasitized by *Cryptosporium epiphyllum* C. and E.—The normal leaf is covered by an epidermis with cells rather larger than those of the sponge tissue. The palisade tissue, which is composed of very long narrow cells, sometimes with a row of short cells below, occupies about half of the total thickness of the leaf. The sponge is very loose and has large air chambers. The cells of the lower epidermis are smaller than those of the upper.

As examined in prepared material, the diseased area is very sharply separated from the healthy part of the leaf. There are practically no cells that show transition phases between the normal and the diseased conditions. The epidermal cells over the parasitized portion are flattened, and often filled with granular deposits which have also been noticed in other diseased plants. The palisade and sponge cells are much shrunken and the entire contents were killed apparently before the specimen was collected. The entire diseased area is yellow-brown, while the normal tissue stains easily with anilin blue. No cytologic changes are to be seen except the deposit of the yellow-brown material throughout

many of the cells, and the occasional enlargement of the nucleus. In some cases the palisade tissue has thus been affected, while the sponge cells are less noticeably changed.

10. XANTHIUM CANADENSE Mill. (?), parasitized by *Puccinia Xanthii* Schu.—The normal leaf tissue is very loosely formed between the upper and the lower epidermal layers. The palisade is scattered, and the sponge is permeated by very large air chambers. Transitional phases between the normal and the diseased conditions of the host cells were not found.

This tissue is more profoundly altered than any other under discussion. It is in many places almost completely replaced by the fungous mycelium. The cells which remain have no protoplasm and are filled with oil globules. On both the upper and the lower leaf surfaces the mycelium is abundant and the telial spores are very numerous. Within the mixture of parenchyma cells and mycelium, which replaces the normal tissue, there are cystlike bodies which are composed of masses of mycelium. These objects are hollow spheres, and from the inner surface arise telial spores exactly similar to those borne in the normal way upon the exterior of the leaf. Part of the mycelium near the exterior stained brown, while that within the host tissue stained blue with anilin blue.

11. ZEA MAYS L., parasitized by *Ustilago Maydis* (DC.) Tul.—The normal host cells are not changed in general appearance, and the general structure of the leaf remains practically normal. Very early in the disease the chloroplasts disappear, but the nuclei remain until very late in the formation of the spores by the smut. In some cases the number of nuclei in a cell is increased, two being the largest number noticed. In this condition the nuclei may also be slightly reduced in size. The nuclei often become deformed, varying from globular to pear-shaped or even crescent-shaped. This deformation seems to be due to mechanical forces at least in part, for in the first place there are cases in which the nucleus is pressed upon on all sides by the forming spores, and the nucleus conforms itself to the rounded shape of the spore walls; in the second place there are nuclei in the diseased area and even in the cells being filled with spores which are normal in shape. If the deformation were due to chemic stimulation, this latter condition

would hardly obtain. The epidermal cells over a diseased region are often filled with a yellowish granular deposit. In the diseased area the cells of the vascular bundle and of the parenchyma alike become filled with a uniform gray plasm, which later breaks up into rounded or hexagonal areas as shown in fig. 9. In the latter stage of the disease these attain more clearly defined walls. It seems evident that these develop eventually into the fungous spores, though the material at hand was not quite old enough to show the last stage of the transformation into the spores. No mycelium was found in the diseased tissue after the formation of the areas mentioned above had begun. It would seem from this that after a certain stage in the disease the fungous mycelium passes into a plastic stage within the host cells, and that then the plastic mass breaks up into spores as previously described. Miss KNOWLES (35) states, in her study of the effect of this same fungus upon the corn stem, that the vegetative mycelium breaks up into masses of smaller filaments which swell up, "except that in many cases, indeed in most cases, the filaments lose their individual form and are more or less blended in a gelatinous, shapeless mass." This gelatinous mass fills the host cells at least in the leaf tissue.

FIG. 9.—One of the outer elements of a vein in a leaf of *Zea Mays* parasitized by *Ustilago Maydis*, showing nucleus and early stage in spore formation within the cell.

12. RAPHANUS SATIVUS L., parasitized by *Albugo canadensis* (Pers.) Kuntze.—The fungus was growing on the cotyledons of young seedlings which were grown in the greenhouse. There is no regular structure to the parenchymatous tissue, as it is all of the ordinary sponge type. There is apparently no great hypertrophy or hyperplasy of the tissues. The blisters seem to be caused by the formation of the mycelium, conidiophores, and conidia just below the epidermis. Few, if any, changes in the cell organs are to be seen. The mycelium is found in abundance. The effect of this fungus seems to be merely that of starvation of the host, not that of poisoning it.

Discussion and conclusions

The changes which are caused in leaf tissue by parasitic fungi are similar to those which have previously been reported as occurring in other parts of phanerogamic plants, and caused by insect invasion, changes of temperature, and parasitic fungi. A comparison of the observations reported in the latter part of this paper with those of other workers reviewed in the earlier part will show that the enlarging, changing of form, and dividing of the nucleus, the changing of the composition of the cell walls, the reduction in the amount of chlorophyll, and other changes in the normal content of the leaf cells are all duplicated in other organs affected by destructive agents.

These changes are usually only variations of natural processes, and are not phenomena that are known only in pathologic tissues, for it is to be noted that these changes in the appearance of the nuclei are not unknown in normal vegetable cells. JOHOW (**33**) describes amitosis as occurring in the older cells of *Chara foetida*. The presence of two or more nuclei in a cell has been noted by TREUB (**78**) in bast cells of various plants; while a process of division is reported by VON BRETFELD (**8**) and MASSART (**42*a***) as so common in wound tissues that they believed nearly all such tissue is formed by the "amitotic" process, as they called it. More detailed work is necessary to show whether the amitotic process of JOHOW and the processes of nuclear division in wound and disease tissues are really analogous, since the former process seems to be for the purpose of increasing the nuclei in connection with the metabolism of mature cells, and the latter processes often lead to an increase in the number of cells, and are found in cells apparently stimulated to a kind of rejuvenescence. SCHÜRHOFF (**67*b***), moreover, has shown that this idea is far from correct, since there are many cases of mitosis in wound tissue, and no true amitosis is certainly known in these tissues. A process that appears to be true amitosis has been reported by SHIBATA (**68**) in mycorhizal cells, and by TISCHLER (**76**) in *Heterodera* galls on *Circaea*. A rather detailed discussion of this question is given by Miss DALE (**15**); while KÜSTER (**40**) and STRASBURGER (**74*b***) review the whole subject of the direct and indirect methods of nuclear division.

No nuclei were noted in actual process of division, but in a few instances there is some evidence of abnormal division. In *Potentilla* (fig. 4) such is the case. The nucleus is somewhat elongated, and at one end is stretched out into a conical point. A comparison of fig. 4 with HÄCKER's (**25***a*) figs. 9, 10, 14, and 16 will show the close resemblance between the nuclei supposed to have divided recently (fig. 4) and the actual process as reported by HÄCKER. A case which is less clearly related is seen in fig. 1, where the nucleus is pear-shaped. Whether or not these are cases of true amitosis or of pseudoamitosis could not be determined, as only the end products were seen.

The composition of the cell walls of the host may be changed. Two evidences of this are forthcoming. In *Panicum*, especially, it was noted that the walls of the parasitized cells are more deeply stained than those of the ordinary cells. Since the walls are not noticeably thickened, the only remaining explanation is that some change in the chemical or physical composition of the walls has taken place, in such a way that they have a greater affinity for the stain, anilin blue. In most of the diseased tissues the walls become brown. This color is probably due to the formation of tannins. There is always more or less of these substances in the walls, and when the cells begin to die, it is known that this browning often takes place through the work of the tannins. In several cases, also, granular deposits were found in various cells in the diseased regions only (of *Castanea*, *Pyrus*, etc.), similar to those described by ZIMMERMAN (**98**, § 207). Just what would cause this precipitation is not clear.

It was not always possible to determine which constituents of the host cell first showed the effect of fungous invasion. It is evident, however, that there is no general rule to be laid down. In *Smilacina*, for example, the chloroplasts seem to disappear before any of the other cell contents, while in *Pyrus* the nuclei of the sponge cells become enlarged before there are any other signs of change. It has already been pointed out that in some cases the cuticle and epidermis are affected first, as the fungus spreads from the center of infection, while in other cases no such result was observed.

The effects of the rust upon the leaf tissue are similar to those of gall-producing insects. The nuclei are enlarged, the protoplasm is often increased, and there is considerable hypertrophy. In other words, the rust seems to stimulate the tissue rather than to retard its growth. The witch brooms are evidences of such an influence, and MOLLIARD (49) describes such effects caused by insects in several hosts.

The effects of the fungous invasion upon the protoplast are various. At times the nuclei may entirely or almost entirely disappear from the diseased areas, leaving the cells, thus deprived of the nucleus, in a dead condition. This was noted in *Potentilla* and *Gaylussacia*. In other cases there is an unusual activity in the nuclear divisions, resulting in several nuclei in one cell. *Viola* and *Panicum* have already been cited as examples of this. The fact has already been given that the nuclei may also become larger than normal. The chromatin content of the diseased nuclei seems at times to become greater also. Such a condition is seen in *Panicum*, in which the nuclei of the diseased cells stain more intensely with hematoxylin than those of the normal cells. This may not be due to an actual increase in the chromatin, but either to a relative increase in the nuclear acid, or to a physical rearrangement of the chromatin. The chloroplasts may be reduced in size and finally disappear, as in *Potentilla*, or they may persist, as in *Viola*, until the final disintegration of the cell. The differences in the reactions of the cytoplasm and of the cell walls have already been cited in other connections.

With the attacks of parasitic fungi on leaves the effects are varied, depending upon the species of the host and of fungus. The virulence of the parasite and the degree of resistance of the host are the chief factors involved. If the leaf, while in actively growing condition, is attacked by the fungus, the changes in the host are often profound, if the fungus is able to maintain itself against the protective measures put in operation by the host. The cytologic changes already described are likely to occur. The leaf curl of peach caused by *Exoascus deformans* is an example of this type of change. Miss KNOWLES (34) has examined the leaf structure in this disease and has found that the tissue is greatly altered

by the presence of the fungus. The leaves are attacked in the bud and very soon after their emergence (DUGGAR 18). Cytologic changes may also occur when the fungus acts slowly for any reason. If the fungus is a weak parasite or if the host is not the best suited to the fungus, the host will have time to react to the fungus, and notable changes may be expected, both in the cell and in the tissue as a whole. That there is a difference in the speed with which various parasites work is seen from the fact that some diseased tissues show cells in various degrees of degeneration or death, while in others there is no intergrading condition between the dead, brown cells of the diseased area and the normal cells of the healthy tissue. The *Gaylussacia* described above shows relatively slow action of the parasite, as is proven by the two following conditions. First, the cells react by showing a granular protoplasm, then a uniform mass of broken-down protoplasm, which is stained brown, and finally nearly empty cell walls. It is improbable that this gradual degeneration is merely a process that would normally take place in cells which are breaking down, because often, as in *Castanea*, none of these intergrading forms are found. Second, it is to be noted that in *Gaylussacia*, and other hosts reacting similarly, the cuticle and the epidermal cells are often affected before the mesophyll, as the fungus spreads from the center of infection. This tends also to prove that the fungus acts progressively and slowly enough to be observed in the successive steps. *Psedera*, *Viola*, and *Panicum* act somewhat similarly in that they show changes in the size and number of nuclei, etc., as cytologic changes induced by the slow action of the respective parasitic fungi. It should be noted in passing, also, that in the case of the rust which was parasitized with *Darluca*, there was a different effect produced upon the nuclei of the leaf cells from that produced by the unparasitized rust. In the latter case the nuclei seem to have disappeared, while in the former case the nuclei are present but very abnormal (fig. 4). It is perhaps significant that nuclei were found only in places where the rust was parasitized, and presumably lowered in its vitality. If the latter statement is true, then the rust would not be able to act so quickly as normally, thus giving the host time to react to its influence.

In some of the diseases described, in which the tissue is killed

in such tissues as the leaves of *Pyrus* and *Xanthium*. Here the hypertrophy is coincident with the changes in the constitution of the cell, and it indicates a rather strong parasitism. On the other hand, as in *Psedera* and *Gaylussacia*, the virulence is so great that the cytologic changes are simply the fleeting features of a rapid degeneration, and of course no hypertrophy could take place. Here again the condition indicates a strong parasitism. TUBEUF (80) points out that the degree of susceptibility of the host, or in other words the degree or strength of parasitism, is indicated by the amount and kind of deformation, as has just been indicated. He draws his illustration from the Uredineae. He says, "If the host suits the fungus only in a limited degree, then no hypertrophy will result, and the latter will attain only to the formation of spermagonia. Let the host, however, be the one best suited to the fungus, then hypertrophy will result and aecidia be developed." He gives as evidence a series of experiments upon *Gymnosporangium*, in which the fungus developed to different degrees varying with the host used. FENSTLING (22), in discussing the effects of rust upon their hosts, comes to the same conclusion regarding the relation of the degree of change to the time of the fungus attack.

In the leaf-inhabiting fungi, so far as studied, the mode of attack seems to be through the aid of some substance injurious or stimulative to the host cells. Two lines of evidence are at hand. The protoplasm of cells outside of the tissue directly in contact with the fungus often becomes killed, and the cell walls become brown. It is difficult to see how such a condition could exist if there is no toxic substance produced. In the second place, most of the cells of the host tissue examined by the writer contained no trace of the fungus, yet, as already shown, the nuclei are often enlarged or become numerous, and the chloroplasts also are reduced in size. Here again, there must be a substance which is diffusible through the cell walls, which is stimulative to the nucleus or poisonous to the chloroplasts. No indications were to be found as to the origin of such a substance. It is possible that the host cells may have produced it as a defensive measure, and that in turn certain of the cells were killed by this toxic substance. On the other hand, it is possible that the fungus may produce such a

poisonous substance which directly affects the host cells, as WARD (86) claims for the *Botrytis* fungus that causes the lily disease. WORONIN (93*b*) attributes in an inferential way the effect of *Sclerotina Vaccinii* upon the cowberry to the same process. TUBEUF (80) quotes from him thus: "Here a peculiar phenomenon is exhibited, the fungus exerts its injurious effects on the *surrounding tissues* of the host plant, then, having killed these, it utilizes them as food material." Thus the tissues are killed first, apparently even beyond the immediate vicinity of the fungus, and are later used for food. That the parasitic fungi upon leaves produce this toxic substance is more easily believed than that the host produces it, and is itself killed by the protective measure. The nature of the poisonous substance, whether a chemical organic poison or an enzyme, could not be determined in the material at hand.

Another interesting question, whose answer may be at least partly suggested, has to do with the strict limitation of certain leaf-inhabiting fungi, such as the shot-hole fungi. This strict limiting of the area of influence of the fungus is shown in the *Smilax* disease described earlier in the paper. At the margin of the diseased area the leaf cells are killed and turned a deep brown to black. This discoloration may be due to the excessive production of tannins, and if so, this would probably explain why the fungus proceeds no farther. BOKORNY (5*b*) has found that tannins will inhibit the growth of fungi, and it seems quite likely that the production of tannins in the leaf finally stops the further growth of the fungus.

Summary

In the review of the previous work, it was found that many changes have been noticed in the organs and tissues of flowering plants. The cytologic changes, however, were especially emphasized. Very little work has previously been reported upon the effect of fungi on the cell contents of leaves, and the writer has shown that in such cells the nuclear and protoplasmic changes, which other workers have noted in cells of other plant organs attacked by parasites or under the influence of other destructive agents, also occur in leaf tissues when attacked by the parasitic fungi examined.

I wish here to thank Dr. T. J. BURRILL of the University of Illinois, under whom these investigations were carried on, for the privileges of the department extended to me, and Dr. CHARLES F. HOTTES of the same department, and Dr. H. A. GLEASON of the University of Michigan, for their kindly criticism of portions of the manuscript.

UNIVERSITY OF TENNESSEE
KNOXVILLE, TENN.

LITERATURE CITED

1. ANDERSON, A. P., Comparative anatomy of the normal and diseased organs of *Abies balsamea* affected with *Aecidium elatinum*. BOT. GAZ. 24:191. 1897.

2. ANDREWS, F. M., Ueber die Wirkung der Centrifugalkraft auf Pflanzen. Jahrb. Wiss. Bot. 38:1. 1902–1903.

3. ———, The effect of gases on nuclear division. Ann. Botany 19:521. 1905.

4. ATKINSON, G. F., Leaf curl and plum pockets. Cornell Exp. Sta. Bull. 73:319. 1894.

5*a*. BLAZEK, J., Ueber den Einfluss der Benzoldämpfe auf die pflanzliche Zellteilung. Abhandl. Böhm. Akad. 2:no. 17. 1902; notes from HOLLRUNG'S Jahresbericht 5:24. 1902.

5*b*. BOKORNY, T., Protection of plants against fungi. Biol. Centralbl. 19: 177–185. 1899; notes from Jour. Roy. Micr. Soc. London 1899:414.

6. BONNIER, G., Expériences sur la production des caractères alpins des plantes par l'altérance des températures extrêmes. Compt. Rend. 127: 307. 1898.

7. ———, Caractères anatomiques et physiologiques des plantes rendues artificielement alpins par l'altérance des températures extrêmes. Compt. Rend. 128:1143. 1899.

8. BRETFELD, F. VON, Ueber Vernarbung und Blattfall. Jahrb. Wiss. Bot. 12:133. 1880.

9. BRUCK, W. F., Zur Frage der Windbeschädigungen an Blättern. Beih. Bot. Centralbl. 20^2:67. 1906.

10. CHAMBERLAIN, C. J., Methods in plant histology. 2d ed. Chicago. 1905.

11. CHODAT, R., Le noyau cellulaire dans quelques cas de parasitisme ou de symbiose intercellulaire. Cong. Internat. Bot. Exp. Univ. Paris. 1900; notes from HOLLRUNG'S Jahresbericht 5:24. 1902.

12. CROCKER, W., and KNIGHT, L. I., Effect of illuminating gas and ethylene upon flowering carnations. BOT. GAZ. 46:259. 1908.

13. DALE, Miss E., On certain outgrowths (intumescences) on the green parts of *Hibiscus vitifolius* Linn. Proc. Camb. Phil. Soc. **10**:192. 1899.

14. ———, Investigations on the abnormal outgrowths or intumescences on *Hibiscus vitifolius*. Phil. Trans. Roy. Soc. B **194**:163. 1901.

15. ———, Further experiments and histological investigations on intumescences, with some observations on nuclear division in pathological tissues. Phil. Trans. Roy. Soc. B **198**:221. 1906.

16. DANGEARD, P. A., Mémoire sur les parasites du noyau et du protoplasma. Le Botaniste **4**:199. 1894–1895.

17. ———, Sur le caryophysème des Eugléniens. Compt. Rend. **131**:1365. 1902.

18. DUGGAR, B. M., Peach leaf curl. Cornell Exp. Sta. Bull. **164**:1899.

19. EBERHARDT, A., Zur Biologie von *Cystopus candidus* Lév. Centralbl. Bakt. **10**²:655. 1903.

20. ———, Contribution à l'étude de *Cystopus candidus* Lév. Centralbl. Bakt. **12**²:235, 426, 614, 714. 1904.

21. FAIRCHILD, D., Ein Beitrag zur Kenntniss der Kernteilung bei *Valonia utricularis*. Ber. Deutsch. Bot. Gesells. **12**:331. 1894.

22. FENSTLING, K., Untersuchungen der durch Rostpilze hervorgerufenen Veränderungen. Inaug. Diss. Freiburg. 1892; notes from SMITH, Forstl. Nat. Zeits. **3**:423.

23. GRANT, A. E., The multinucleated condition of the vegetative cell, with some special researches relating to cell morphology. Trans. Bot. Soc. Edinburgh **16**:38. 1883.

24. GUTTENBERG, H., Beiträge zur physiologischen Anatomie der Pilzgallen. Leipsic. 1905.

25*a*. HÄCKER, V., Mitosen im Gefolge amitosenähnlicher Vorgänge. Anat. Anz. **17**:9. 1900.

25*b*. HALSTED, B. D., Starch distribution as affected by fungi. Proc. Am. Ass. Adv. Sci. **47**:408. 1898.

26*a*. HANSEN, A., Experimentelle Untersuchungen über die Beschädigungen der Blätter durch Wind. Flora **93**:32. 1904.

26*b*. HARTIG, R., Wichtige Krankheiten d. Waldbäume. 1874; notes from TUBEUF (see 80).

27. HARTMANN, F., Anatomische Vergleichung der Hexenbesen der Weisstanne mit der normalen Sprossen derselben. Inaug. Diss. Freiburg. 1892; notes from SMITH, Forst. Nat. Zeits. **3**:421.

28. HOWARD, C., Sur l'accentuation des caractères alpins des feuilles dans les galles des Genévriers. Compt. Rend. **140**:56. 1905.

29. ———, Modifications histologiques produites par des *Copium* dans les fleurs des *Teucrium*. Marcellia **5**:83. 1906; notes from Centralbl. Bakt. **20**²:201. 1908.

30. ———, Sur l'anatomie de la galle de l'involucre des Euphorbes. Rev. Gén. Bot. **18**:67. 1906.

31. HOWARD, C., Anatomie de la "Galle en Capsule" de l'*Euphorbia Cyparissias* L. Rev. Gén. Bot. **18**:241. 1906.

32. ———, Sur les modifications histologiques apportées aux fleurs du *Teucrium Chamaedrys* et du *T. montanum* par les larves de *Copium*. Compt. Rend. **143**:927. 1906.

33. JOHOW, F., Ueber die Zellkerne von *Chara foetida*. Bot. Zeit. **39**:729, 745. 1881.

34. KNOWLES, Miss E. L., The "curl" of peach leaves; *Exoascus deformans*. BOT. GAZ. **12**:216. 1887.

35. ———, A study of the abnormal structures induced by *Ustilago Zeae Mays*. Jour. Mycol. **5**:14. 1889.

36. KOHL, F. G., Zur Physiologie des Zellkernes. Bot. Centralbl. **72**:168. 1897.

37. KÜSTER, E., Beiträge zur Kenntniss der Gallenanatomie. Flora **87**:117. 1900.

38. ———, Pathologische Pflanzenanatomie. Jena. 1903.

39. ———, Beiträge zur Physiologie und Pathologie der Pflanzenzelle. Zeits. Allg. Physiol. **4**:221. 1904.

40. ———, Neue Ergebnisse auf dem Gebiet der pathologischen Pflanzenanatomie. Ergebn. Allg. Path. u. Path. Anat. **11**:387. 1906.

41. MAGNUS, W., Studien an der endotrophen Mycorrhiza von *Neottia Nidus-avis* L. Jahrb. Wiss. Bot. **35**:205. 1900.

42*a*. MASSART, J., Cicatrisation chez les végétaux. Mém. Acad. Belg. **57**:3. 1898.

42*b*. MASSEE, G., On the origin of parasitism in fungi. Phil. Trans. Roy. Soc. **197**:7–23. 1905.

43. MEEHAN, T., On the influence of fungi on the form and character of plants. Proc. Acad. Nat. Sci. Phila. 1899:108.

44*a*. MIEHE, H., Ueber die Wanderungen des pflanzlichen Zellkernes. Flora **88**:105. 1901.

44*b*. MIYOSHI, M., Die Durchbohrung von Membranen durch Pilzfaden. Jahrb. Wiss. Bot. **28**:269–289. 1895.

45. MATRUCHOT, L., and MOLLIARD, M., Sur certains phénomènes présentés par les noyaux sur l'action du froid. Compt. Rend. **130**:788. 1900.

46. ———, Modifications de structure observées dans les cellules subissants la fermentation propre. Compt. Rend. **130**:1203. 1900.

47. ———, Modifications produites par le gel dans la structure des cellules végétables. Rev. Gén. Bot. **14**:401, 463, 522. 1902.

48. MOLLIARD, M., Recherches sur les Cécidies florales. Ann. Sci. Nat. Bot. VIII. **1**:67. 1895.

49. ———, Hypertrophie pathologique des cellules végétales. Rev. Gén. Bot. **9**:33. 1897.

50. ———, Note de pathologie végétales. Rev. Gén. Bot. **10**:87. 1898.

51. MOLLIARD, M., Sur les modifications histologiques produites dans les tiges par l'action des *Phytoptus*. Compt. Rend. 129:841. 1899.

52. ———, Sur quelques caractères histologiques des cécidies produites par l'*Heterodera radicicola* Greff. Rev. Gén. Bot. 12:157. 1900.

53. NATHANSOHN, A., Physiologische Untersuchungen über amitotische Kerntheilung. Jahrb. Wiss. Bot. 35:48. 1900.

54. NAWASCHIN, S., Beobachtungen über der feineren Bau und Umwandlungen von *Plasmodiophora Brassicae* Wor. im Laufe ihres intrazellularen Lebens. Flora 86:404. 1890.

55. NĚMEC, B., Cytologische Untersuchungen an Vegetationspunkten der Pflanzen. Sitzungsb. Königl.-Böhm. Gesells. Wiss. no. 23. 1897.

56. ———, Ueber abnorme Kerntheilungen in der Wurzelspitze von *Allium Cepa*. Sitzungsb. Königl.-Böhm. Gesells. Wiss. no. 4. 1898.

57. ———, Ueber den Einfluss niedriger Temperaturen auf meristematische Gewebe. Sitzungsb. Königl.-Böhm. Gesells. Wiss. no. 12. 1899.

58*a*. ———. Ueber ungeschlechtliche Kernverschmelzungen. Sitzungsb. Königl.-Böhm. Gesells. Wiss. 1902; notes from HOLLRUNG's Jahresbericht. 1902.

58*b*. ———, Ueber ungeschlechtlicher Kernverschmelzung. Siztungsb. Königl.-Böhm. Gesells. Wiss. no. 59. 1902; no. 27, 1903; no. 42, 1903; no. 13, 1904.

59. ———, Ueber die Einwirkung des Chlorohydrats auf die Kern- und Zelltheilung. Jahrb. Wiss. Bot. 39:645. 1903–1904.

60. ———, Ueber Regenerationsercheinungen an angeschnittenen Wurzelspitzen. Ber. deutsch. bot. Gesells. 23:113. 1905.

61. NORDHAUSEN, M., Beiträge zur Biologie parasitärer Pilze. Jahrb. Wiss. Bot. 33:1. 1898.

62. PARATONE, E., Ricerche sulla strattura e le alterazioni del nucleo nei tubercoli radicoli delle Leguminose. Malphigia 15:178. 1901; notes from HOLLRUNG's Jahresbericht 5:24. 1902.

63. PEGLION, V., Ricerche anatomiche sopra i tumori delle foglie e rami di Pero causati dal parassitismo della *Roestelia cancellata*. Rivista Path. Veg. 2:23. 1893; notes from Bot. Centralbl. 56:339. 1893.

64*a*. PEIRCE, G. J., The root tubercles of bur clover (*Medicago denticulata* Willd.) and some other leguminous plants. Proc. Cal. Acad. Sci. III. Bot. 2:295. 1902; notes from STRASBURGER, Prog. Rei Bot. 82. 1906.

64*b*. PERCIVAL, JOHN, Potato "wart" disease; the life history and cytology of *Synchytrium endobioticum* (Sc.) Percl. Centralbl. Bakt. 25^2:440–447. 1909.

65. PRILLIEUX, E., Alterations produites dans les plantes par la culture dans un sol surchauffé. Ann. Sci. Nat. Bot. VI. 10:347. 1880.

66. SCHRAMMEN, F. R., Ueber die Einwirkungen von Temperaturen auf die Zellen des Vegetationspunkt des Sprosses von *Vicia Faba*. Bonn. 1902; notes from HOLLRUNG's Jahresbericht. 1902.

67a. SCHRENK, H. VON, Intumescences formed as a result of chemical stimulation. Rep. Mo. Bot. Gard. **16**: 125. 1905.

67b. SCHÜRHOFF, P., Das Verhalten des Kernes im Wundgewebe. Beih. Bot. Centralbl. **19**[1]: 359. 1906.

68. SHIBATA, K., Cytologische Studien über die endotrophen Mykorrhizen. Jahrb. Wiss. Bot. **37**: 643. 1902.

69. SMITH, G., The haustoria of the Erysipheae. BOT. GAZ. (1900) **29**: 153. 1900.

70. SMITH, W. G., Untersuchung der Morphologie und Anatomie der durch Exoasceen verursachten Spross und Blattdeformationen. Forst. Nat. Zeitsch. **3**: 420, 433, 473. 1894.

71. SORAUER, P., Ueber Intumescenzen. Ber. Deutsch. Bot. Gesells. **17**: 456. 1899.

72. ———, Intumescenzen an Blüthen. Ber. Deutsch. Bot. Gesells. **19**: 115. 1901.

73. STEINER, R., Ueber intumescenzen bei *Ruellia formosa* Andrew and *Aphelandra Porteana* Morel. Ber. Deutsch. Bot. Gesells. **23**: 105. 1905.

74a. STRASBURGER, E., Das botanische Practicum. Jena. 1902.

74b. ———, Die Ontogenie der Zelle zeit 1875. Prog. Rei Bot. **1**: 1. 1906.

75. STROHMEYER, O., Anatomische Untersuchung der durch Ustilagineen hervorgerufenen Missbildungen. Diss. Erlangen. 1896; notes from MOLLIARD, Rev. Gén. Bot. **10**: 92. 1898.

76. TISCHLER, G., Ueber *Heterodera*-Gallen an den Wurzeln von *Circaea Lutetiana* L. Ber. Deutsch. Bot. Gesells. **19**: 95. 1901.

77. TOUMEY, J. W., An inquiry into the cause and nature of crown-gall. Arizona Exp. Sta. Bull. 33. 1900.

78. TREUB, M., Sur les cellules végétales à plusieurs noyaux. Archiv Néerland. Sci. **15**: 39. 1880; notes from TREUB, Compt. Rend. **89**: 494. 1879.

79. ———, Quelques mots sur les effets du parasitisme de l'*Heterodera javanica* dans les racines de la canne à sucre. Ann. Jard. Bot. Buit. **6**: 93. 1886; notes from STRASBURGER, Prog. Rei Bot. 82. 1906.

80. TUBEUF, K. F. VON, Diseases of plants induced by cryptogamic parasites. Engl. transl. by W. G. SMITH. London. 1897.

81. UNGER, F., Beiträge zur Anatomie u. Physiologie der Pflanzen. Sitzungsb. K. Akad. Wiss. Wien **50**: 132. 1864.

82. VUILLEMIN, P., and LEGRAIN, E., Symbiose de l'*Heterodera radicicola* avec les plantes cultinées au Sahara. Compt. Rend. **118**: 549. 1894.

83. WAGNER, A., Zur Kentniss des Plattbaues der Alpenpflanzen und dessen biologischen Bedeutung. Sitzungsb. K. Akad. Wiss. Wien. 101. 1892.

84. WAKKER, J. H., Untersuchungen über Einfluss parasitischer Pilze auf ihre Nährpflanzen. Jahrb. Wiss. Bot. **24**: 499. 1892.

85. WASIELEWSKI, W. VON, Theoretische und experimentelle Beiträge zur Kentniss der Amitiosis. Jahrb. Wiss. Bot. 38:377. 1902–1903; 39:581. 1903–1904.
86. WARD, H. M., A lily disease. Ann. Botany 2:319. 1888–1889.
87. ———, On some relations between host and parasite, etc. Proc. Roy. Soc. London 47:393. 1890.
88. ———, Recent researches on the parasitism of fungi. Ann. Botany 19:1. 1905.
89. WILFARTH, N., and WIMMER, G., Die Wirkungen der Stickstoff, Phosphorsäure, und Kalimangels auf die Pflanzen. Jour. Landw. 51:129. 1903.
90. ———, Die Kennzeichen des Kalimangels an den Blättern der Pflanzen. Zeits. Pflanzkr. 13:82. 1903.
91. WISSELINGH, C. VAN, Ueber abnormale Kernteilung: fünfter Beitrag zur Karyokinese. Blätt. Zuckerrübenbau 61:201. 1903; notes from HOLLRUNG'S Jahresbericht 6:16. 1903.
92. WOODS, A. F., Plant pathology. Science 26:554. 1907.
93*a*. WORONIN, M., *Exobasidium Vaccinii.* Ber. Naturf. Gesells. Freiburg. 1867; notes from SMITH, Forst. Zeits. 3:422.
93*b*. ———, Ueber die Sclerotienkrankheit der Vaccinieenbeeren. Mém. Acad. Imp. Sci. St. Pétersbourgh 36:1888.
94*a*. WÖRNLE, P., Anatomische Untersuchung der durch *Gymnosporangium*-Arten hervorgerufenen Missbildungen. Forst. Naturw. Zeitsch. 3:68, 129. 1894.
94*b*. ZACH, FRANZ, Studie über Phagocytose in den Wurtzelknöllchen der Cycadeen. Oesterr. Bot. Zeitsch. 60:49–55. 1910; notes from Centralbl. Bakt. 27^2:677. 1910.
95. ZACHARIAS, E., Ueber das Verhalten des Zellkerns in wachsenden Zellen. Flora 81:217. 1895.
96. ZIMMERMAN, A., Die Morphologie und Physiologie der Pflanzenzelle. SCHENCK'S *Handbuch der Botanik* 3:1887.
97. ———, Die Morphologie und Physiologie des pflanzlichen Zellkernes. Jena. 1896.
98. ———, Botanical microtechnique. Engl. transl. by J. E. HUMPHREY. 1896.

THE INFLUENCE OF THE SEED UPON THE SIZE OF THE FRUIT IN STAPHYLEA. II

J. ARTHUR HARRIS

(WITH ONE FIGURE)

IV. On the nature of the correlation between the number of seeds and pod length

Heretofore we have contented ourselves with such analysis of our data as is necessary to the establishment on a sound quantitative basis of the fact of a correlation between the number of seeds developing and the length of the pod. This correlation is that of the statistician, not of the physiologist. It shows the existence of a relationship between two characters and measures its intensity. It does not prove that this relationship is due to a direct physiological interdependence between the two characters. To demonstrate such physiological interdependence one must remove the influence of other possible factors. All of the factors which seem possible sources of the correlation between the number of seeds developing and pod length and which can be investigated on the available data are discussed below.

1. THE HYPOTHESIS OF THE INFLUENCE OF THE RELATIONSHIP FOR OVULES AND LENGTH

As emphasized in the paper on *Cercis*, one of the sources of confusion in interpreting an observed r_{ls} is the fact that both l and s may be correlated with o, and so differences in the fruit length (l) which appear to be due directly to the number of seeds developing may be merely resultants of the relationship r_{lo} and r_{os}, and so indicate no physiological relationship between s and l. But it has been conclusively shown that $r_{ls} > r_{lo}$, thus demonstrating that the interdependence for seeds and length is not solely dependent upon the relationship for ovules and length. Indeed, it is only when both r_{lo} and r_{os} are high that they will greatly affect r_{ls}. It seems desirable, however, not to leave the question without showing just how much influence may be attributed to this factor. I use the two methods suggested in the paper on *Cercis*, namely, the corre-

lation for length and seed/ovule index and the partial correlation coefficient. Comparing r_{ls} and r_{li} for the combined series we have:

Relationship	1906—2050 pods	1907—1218 pods
Number of seeds and length, r_{ls}....	0.3522±0.0131	0.2019±0.0185
Seed/ovule index and length, r_{li}....	0.3418±0.0132	0.2018±0.0185
Difference, $r_{ls}-r_{li}$............	0.0104±0.0186	0.0001±0.0261

Both differences are less than their probable errors, and of no significance.[1]

Consider now the correlation between s and l for constant values of o, as measured by the partial correlation coefficient of ρ_{ls}. The correlations for number of ovules formed and number of seeds developing per locule (r_{os}) are necessary. The tables of data are 36 in number, and since they are supplementary rather than fundamental to our main subject, we need not publish them. The constants with their probable errors are set forth in tables XI and XII.

TABLE XI

Number of shrub	r_{os} Correlation, ovules and seeds	r/E_r
11.......	−0.076±0.037	2.06
12.......	0.042±0.035	1.19
13.......	0.154±0.037	4.16
14.......	0.112±0.038	2.96
15.......	−0.131±0.037	3.54
16.......	−0.063±0.039	1.61
17.......	0.080±0.039	2.05
18.......	0.002±0.039	0.05
19.......	−0.038±0.039	0.96
20.......	0.045±0.037	1.20
21.......	−0.094±0.039	2.40
22.......	0.028±0.039	0.71
23.......	0.014±0.039	0.36
24.......	0.144±0.038	3.78
25.......	0.078±0.039	2.00
26.......	0.026±0.039	0.67
27.......	0.048±0.039	1.22
28.......	0.093±0.038	2.45
29.......	0.058±0.039	1.48
30.......	0.042±0.039	1.08

TABLE XII

Number of shrub	r_{os} Correlation, ovules and seeds	r/E_r
11.......	0.156±0.060	2.60
17.......	0.021±0.054	0.39
19.......	−0.072±0.046	1.56
24.......	0.159±0.038	4.23
29.......	0.028±0.047	0.60
31.......	0.057±0.038	1.50
32.......	0.094±0.043	2.18
33.......	0.126±0.126	3.19
34.......	0.025±0.025	0.56
35.......	0.079±0.079	1.73
36.......	0.150±0.049	3.08
37.......	0.004±0.040	0.10
38.......	0.033±0.040	0.82
39.......	0.137±0.059	2.33
40.......	0.045±0.039	1.16
41.......	0.010±0.050	0.19

[1] Possibly we are not quite justified in using the ordinary method of calculating the probable error of a difference here, that is, the square root of the sum of the squares of the two probable errors, but the differences in the correlation are so very small that it makes no practical difference.

In 1906, 15 of the constants have the positive and 5 the negative sign; in 1907, only one of the 16 is negative. Throughout, the values are too low to be of any practical significance. The mean for 1906 is 0.0282, and for 1907 it is 0.0658. We have already found low values for r_{lo}, and with the very small values for r_{so} just demonstrated, it seems hardly worth while to calculate ρ_{ls}. But, using the formula $\rho_{ls}=\frac{r_{ls}-r_{lo}r_{so}}{\sqrt{1-r_{lo}^2}\sqrt{1-r_{so}^2}}$, and substituting the mean values of the constants for the individuals as the most trustworthy measures for the physiologist, we find:

Relationship	1906—20 shrubs	1907—16 shrubs
Average r_{lo}	0.1282	0.1240
Average r_{so}	0.0282	0.0658
Average r_{ls}	0.3868	0.3636
Calculated ρ_{ls}	0.3865	0.3591
$r_{ls}-\rho_{ls}$	0.0003	0.0045

Obviously there is no practical significance whatever to be attached to the differences such as 0.0003 and 0.0045. In *Cercis*, r_{ls} is very materially reduced when allowance is made for the influence of the number of ovules. The two foregoing methods show that in *Staphylea* r_{ls} is essentially independent of r_{lo} and r_{so}.

2. THE HYPOTHESIS OF MECHANICAL STRETCHING

Where the seeds in a locule attain a considerable size and are numerous, it is quite possible that an increased size of the fruit might result from their space requirements, through the purely mechanical effects of crowding. In *Cercis* the seeds are relatively small and, generally at least, not in contact. Mechanical stretching seemed almost entirely excluded by the nature of the material, and I gave no attention to it. In *Staphylea* there seems even less reason to suppose this factor to be of any importance, but it is well to have such conclusions based on actual statistics. To test whether there is a sensible influence of the spatial requirements of the seeds upon the length of the pods, I think we may proceed as follows.

Clearly there can be little mechanical stretching of the placental space due to the development of a single seed in a locule. All the

room which it demands is that necessary for its attachment; the pressure of adjoining seeds is a factor entirely removed. *Staphylea* has the advantage that the number of seeds developing is so small that it is easy to select material in which the stretching of the pod by a crowding of the seeds can hardly be a possibility. For pods with one to three seeds, there may be only a single seed in each

TABLE XIII

Class	1906		1907	
	f	Mean length	f	Mean length
1 Seed				
1–0–0	960	5.57	519	6.26
2 Seeds				
1–1–0	291	6.39	227	6.83
2–0–0	204	6.46	105	6.96
3 Seeds				
1–1–1	57	7.23	32	7.19
2–1–0	172	6.97	117	7.21
3–0–0	47	7.21	26	6.96
4 Seeds				
2–1–1	64	7.56	40	7.38
2–2–0	33	7.39	15	7.33
3–1–0	39	7.90	23	7.61
4–0–0	14	7.64	5	7.80

locule, that is, seed formulae: 1–0–0, 1–1–0, 1–1–1. When more than three are produced, one of the locules must have two or more. Now the problem is simply this; given fruits producing the same number of seeds, are those in which two or more of the seeds are produced in the same locule larger than those in which but a single seed is produced in each locule?

Table XIII gives the number of pods available and the mean length of pod for the chief seed-formulae (including about 91 per cent of the whole number of fruits available) for the 1906 and 1907 series. The results are also shown graphically in fig. 5. Here the solid dots give the empirical means for the individual seed-formulae for 1906 and the circles those for 1907. The vertical lines (solid for 1906 and broken for 1907) indicate the mean length of pods with 1, 2, 3, and 4 seeds per pod, irrespective of the distribution of these seeds among the locules. Certainly there is no clear evidence in this figure that pods in which the seeds are grouped in less than

three locules are longer than those in which they are as much distributed as possible among the three. It follows that mechanical

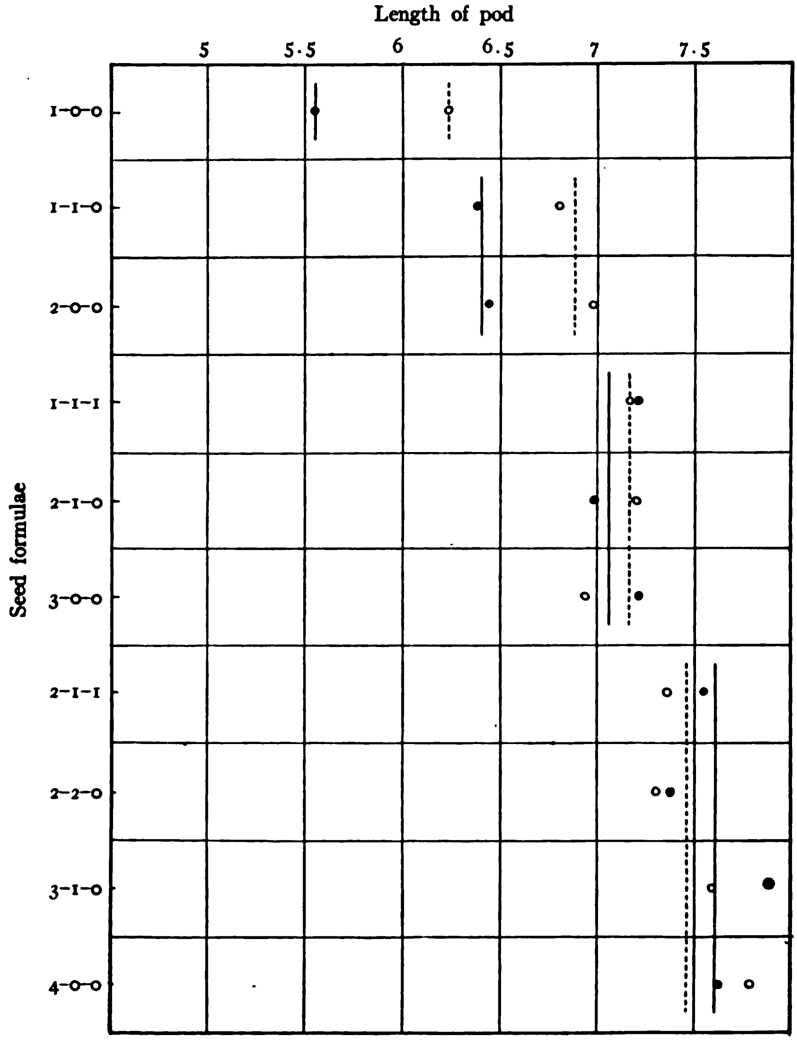


FIG. 5.—Mean lengths of pod for different seed-formulae and total number of seeds per fruit; solid dots and lines = 1906; circles and broken line = 1907.

stretching of the pod has had little or no part in the bringing about of the correlation between length and number of seeds developing.

3. THE HYPOTHESIS OF THE MUTUAL DEPENDENCE OF FRUIT LENGTH AND FERTILITY UPON OTHER CHARACTERS OF THE PLANT

Two characters both positively or negatively correlated with a third are correlated with each other. This is doubtless the source of much of the correlation found between organs. Possibly r_{lo} and r_{ls} indicate no physiological interdependence between l and o or l and s, but are due merely to l, o, and s being influenced by the position of the fruit on the inflorescence or by the number of pods per inflorescence. The correlation between the length of the pod and the distance of the flower-bearing node at which it is produced from the base of the inflorescence[2] is shown for the 1906 series[3] in table XIV, 1906, and for number of pods developing per inflorescence and length of pod in table XV, 1906. These give:

Position and length, $r_{pl} = -0.0580 \pm 0.0148$
Number and length, $r_{nl} = -0.1828 \pm 0.0144$

Statistically these values are certainly trustworthy, for $r_{pl}/E_r = 3.91$, and $r_{nl}/E_r = 12.70$. They indicate that both a more distal position on the inflorescence and a number of fruits above the normal is prejudicial to the maximum development of the fruit.[4]

If it be found that the number of seeds developing is also negatively correlated with the position and with the number of the

TABLE XIV, 1906

LENGTH OF FRUIT

Position	3	4	5	6	7	8	9	10	11	Totals
1.......	1	65	192	322	259	125	62	20	1	1047
2.......	4	50	167	197	143	88	31	9	..	689
3.......	1	25	69	75	54	31	14	2	..	271
4.......	..	2	9	13	6	4	5	1	..	40
5.......	..	..	...	3	...	...	...	..	..	3
Totals	6	142	437	610	462	248	112	32	1	2050

[2] The serial position of the node on the inflorescence counting from the base.

[3] Data for position are not available for 1907. Because of a severe frost many of the inflorescences produced only a single fruit, and it seems idle to study the number per inflorescence.

[4] Inflorescences with larger numbers of fruits will have more distally placed fruits. I have not worked out the correlation between these two characters, but if it is considerable the two constants just discussed are not independent, and probably one or both should be, biologically considered, more nearly 0.

TABLE XV, 1906

LENGTH OF FRUIT

Fruits in infl.	3	4	5	6	7	8	9	10	11	Totals
1	..	..	..	..	1	..	..	..	..	1
2	..	8	36	44	59	40	26	8	1	222
3	1	22	85	167	127	66	41	8	..	517
4	2	38	120	166	112	73	28	10	..	549
5	1	40	90	115	88	42	7	2	..	385
6	1	31	65	61	34	14	6	3	..	215
7	..	2	20	20	21	7	4	1	..	75
8	1	1	13	28	10	3	..	..	..	56
9	..	..	2	2	4	1	..	..	..	9
10	..	..	3	3	2	1	..	..	..	9
11	..	..	..	..	..	..	..	..	..	..
12	..	..	3	4	4	1	..	..	..	12
Totals	6	142	437	610	462	248	112	32	1	2050

fruits developing on an inflorescence, we should expect a positive correlation between number of seeds developing and length of pod, due to no direct physiological interdependence of the two, but solely to their correlation with these other characters. Turning to our data, we see the correlation surface for position and seeds per locule in table XVI, 1906, and between number per inflorescence and seeds per locule in table XVII, 1906. To the eye there seems to be little or no correlation. The calculating machine shows:

For position of fruit and seeds, $r_{ps} = -0.0148 \pm 0.0149$

For number of fruits and seeds, $r_{ns} = -0.0474 \pm 0.0148$

Again the signs are negative, but the values are so low that little importance can be safely attached to them.

With such low correlations, it seems hardly worth while to consider the amount of influence which position on the inflorescence or number of pods per inflorescence would have upon the degree of interdependence of *s* and *l*, but since biometricians are frequently criticized for neglecting just such biological considerations as this, I calculated the correlation for seeds and length for constant numbers of pods per inflorescence. Number rather than position was chosen, since the correlations are numerically higher and will have greater influence on r_{sl}. Working from the formula

$$\rho_{sl} = \frac{r_{sl} - r_{ns} \cdot r_{nl}}{\sqrt{1 - r_{ns}^2}\,\sqrt{1 - r_{nl}^2}},$$

we find:

$$r_{sl}=0.3522\pm0.0131,$$
$$\rho_{sl}=0.3498\pm0.0131,$$

$$r_{sl}-\rho_{sl}=0.0024\pm0.0185$$

TABLE XVI, 1906

SEEDS PER LOCULE

Position	0	1	2	3	4	5	6	Totals
1	1533	1109	355	115	33	11	..	3156
2	1076	733	190	60	16	4	..	2079
3	404	285	88	28	7	1	..	813
4	56	40	12	9	2	..	1	120
5	5	3	1	....	..	..	..	9
Totals	3074	2170	646	212	58	16	1	6177

TABLE XVII, 1906

SEEDS PER LOCULE

Fruits per infl.	0	1	2	3	4	5	6	Totals
1	2	....	1	....	..	..	..	3
2	299	238	82	29	14	4	..	666
3	761	556	170	54	15	4	..	1560
4	827	581	164	60	16	5	..	1653
5	591	399	120	37	7	1	..	1155
6	343	217	63	17	5	2	1	648
7	115	85	25	6	..	..	..	231
8	91	61	13	2	1	..	..	168
9	10	14	2	1	..	..	..	27
10	14	10	2	4	..	..	..	30
11	....	....	....	....	..	..	..	....
12	21	9	4	2	..	..	..	36
Totals	3074	2170	646	212	58	16	1	6177

The reduction in correlation is only about one-eighth of the probable error of the determination! Further arithmetic or discussion would be pedantic. I conclude that the correlation between the number of seeds developing and the length of the fruit is not merely a secondary result of the correlation of these two characters with position on the inflorescence or number of pods per inflorescence, but must be due to some force operating in the developing fruit itself.

For *Cercis* I have no data for the relationship between the number of pods per inflorescence and the fertility and length characters

of the fruits, but it may be of some interest to determine the correlation between the number of ovaries and the number of ovules per ovary for the three series of intact inflorescences gathered in the spring of 1907.[5] The data for r_{no} are given in tables XVIII and XIX.[6] The coefficients of correlation[7] are

Tree 1, $r = -0.007 \pm 0.023$
Tree 2, $r = 0.030 \pm 0.021$
Tree 3, $r = 0.134 \pm 0.024$

In the first two cases the correlations are certainly insignificant. In the third tree there is a slight correlation which is about six times its probable error. Ordinarily this would be considered trustworthy, but the actual number of ovaries instead of the

TABLE XVIII, CERCIS

Ovaries per inflorescence	Tree 1		Tree 2		Tree 3	
	Number of ovaries	Total ovules	Number of ovaries	Total ovules	Number of ovaries	Total ovules
5	...	...	5	27	25	125
6	6	44	...	...	112	532
7	84	647	...	...	139	672
8	197	1515	15	76	214	1043
9	176	1344	26	146	181	895
10	209	1585	130	679	49	243
11	142	1095	283	1495	11	60
12	47	359	297	1596	...	...
13	...	...	168	897	...	...
14	27	207	139	763	14	75
15	...	...	15	89	...	...
16	...	...	...	...	...	...
17	...	...	...	...	17	92
Totals	888	6796	1078	5768	762	3737

[5] HARRIS, J. ARTHUR, Is there a selective elimination of ovaries in the fruiting of the Leguminosae? Amer. Nat. **43**:556–559. 1909.

[6] Again the different inflorescence grades are necessarily weighted with the number of flowers which they bear, and the means and standard deviations used in determining the coefficients of correlation are calculated from these weighted frequencies. SHEPPARD'S correction was not used. The single case of no ovules is probably due to one of the ovaries being still too young. In dissecting the ovaries out of the flowers, clearing, and examining under the lens, some accidents are unavoidable. There is no reason to believe that the 35 ovaries which were broken or ruined in clearing differed from those which could be counted. They are simply omitted in the calculations.

[7] Calculated by method described in Amer. Nat. **44**:693–699. 1910.

TABLE XIX, CERCIS

NUMBER OF OVULES PER OVARY

	0	1	2	3	4	5	6	7	8	9	10
Tree 1........	..	..	..	..	3	1	49	279	476	76	4
Tree 2........	1	1	5	32	177	327	431	100	4	..	..
Tree 3........	..	..	10	23	198	341	179	11	..	..	..

number of inflorescences was used in calculating the probable error. This is perhaps justifiable, but had N been taken as 100, the actual number of inflorescences, the probable error would have been much higher, and in the third tree the correlation would have been only about twice or thrice its probable error. On the basis of available data, there is no demonstrable relationship, therefore, between the number of ovaries on an inflorescence and their characteristics.

4. THE HYPOTHESIS OF THE INDIVIDUALITY OF INFLORESCENCES

It has now been shown that neither position nor number of pods has sufficient relationship with the two characters immediately under consideration to produce a sensible correlation between them. Theoretically both p and n would influence, to some extent, the quantity of plastic material available for a given fruit, but so far as these evidences go, similarity of nutrition for both seeds and fruit wall has little influence in bringing about the correlation between them. These are not the only factors which might influence the food supply of a developing fruit. Some inflorescences may be much more generously supplied with fruit and seed building substances than others, and in the distribution of this material throughout the inflorescence, position of pod may have a negligible significance, and number of pods developing be of only small importance.

I believe the following method to be satisfactory in determining whether r_{ls} is due to the differentiation between the inflorescences of an individual either (a) in the capacity for development of the protoplasm of which their ovaries are made up, or (b) in the availability of food material for the expansion of these organs.

If both the pod length and the number of seeds developing are influenced by the nature of the inflorescence upon which they are

borne, or by the quantity of the plastic material which it receives from the shrub, in a way to bring about a correlation between the length of a pod and the seeds which it matures when the pods from an individual are used as a sample, there should be a correlation between the number of seeds developing in a fruit and the length of another fruit on the same inflorescence. In short, if there is something inherent in the inflorescence which tends to influence both number of seeds developing and length of fruit in the same sense, so that a correlation arises between them, this influence should effect in some degree all pods with the result that the cross correlation between number of seeds developing in one pod and length of another pod should have a sensible positive value.

The only disadvantage of this method is its extreme laboriousness. It is necessary to draw up tables between the characters of the fruits of the same inflorescence, just as in a study of heredity one prepares tables showing the correlation between brothers in the same family. Each pod is used once in association with every other pod on the same inflorescence. The number of combinations thus secured will be $\frac{1}{2}n(n-1)$, and since for practical purposes we use each fruit once as a first and once as a second member of an associated pair,[8] we have for each inflorescence $n(n-1)$ combinations.

All inflorescences have not the same number of pods, and an inflorescence with six locules will give relatively fewer entries in the symmetrical table than one with twelve. I regret the necessity of thus giving weight to the larger inflorescences, but since the

[8] For the intra-inflorescence relationship for the length of the fruit it is only necessary to draw up tables showing all possible combinations of the fruit lengths of the same inflorescence. But for ovules and seeds we are dealing with the individual locules, and there are three to each fruit. If we made every possible combination in the preparation of the tables, we would be correlating, in some cases, between the locules of the same fruit, and, in some cases, between the locules of different fruits on the same inflorescence. The point which we wish to get at is the relationship between the different fruits of the same inflorescence. The plan followed, therefore, has been to correlate the number of ovules formed or the number of seeds developing in each locule with the number in every other locule on the inflorescence, except those of the same fruit. In the same manner, in dealing with the relationships between length of pod and the fertility characters, the tables were so drawn as to show the relationship between the length of the pod and the fertility characters of all the locules on the inflorescence, except its own three.

correlations between the number of pods per inflorescence and all the characters of the pod are generally very low, it hardly seems worth the labor to reduce all the inflorescences to a standard frequency to avoid weighting. Designating the two characters of a pair which are being compared as "first" and "second," and indicating them by one and two dashes respectively, we have the following relationships for consideration.

Ovules of first locule and ovules of second locule, $r_{o'o''}$
Seeds of first locule and seeds of second locule, $r_{s's''}$
Length of first pod and length of second pod, $r_{l'l''}$
Length of first pod and ovules per locule in second pod, $r_{l'o''}$
Length of first pod and seeds per locule in second pod, $r_{l's''}$

Since the pods from each shrub must be treated separately, this requires the preparation of 100 correlation tables, containing some hundreds or thousands of entries each. These have been carefully prepared and verified, and the means and standard deviations used in obtaining the correlation coefficients calculated anew for all the characters from the weighted frequencies. The tables and constants are too bulky for publication. The end results

TABLE XX

INTRA-INFLORESCENCE CORRELATION COEFFICIENTS

Shrub	Ovules of first locule and ovules of second locule	Seeds of first locule and seeds of second locule	Length of first pod and length of second pod	Length of first pod and ovules per locule in second pod	Length of first pod and seeds per locule in second pod
11	0.516	0.098	0.517	−0.387	0.190
12	0.037	0.004	−0.003	−0.217	−0.091
13	0.078	−0.025	0.009	0.051	−0.008
14	0.093	−0.017	0.017	0.027	0.008
15	0.113	0.034	0.178	0.049	0.046
16	0.088	−0.009	0.113	0.083	−0.030
17	0.108	0.017	0.244	0.317	0.008
18	−0.026	−0.028	−0.045	0.020	−0.087
19	0.084	−0.017	−0.036	−0.068	−0.020
20	0.123	0.031	0.109	0.074	0.049
21	0.143	0.003	0.052	−0.067	0.000
22	0.026	0.020	0.059	0.007	0.039
23	0.084	0.015	0.018	−0.031	−0.014
24	0.093	−0.034	−0.007	0.010	−0.052
25	0.515	0.096	0.378	0.206	0.183
26	0.099	0.042	0.115	0.044	0.062
27	0.059	−0.038	0.058	0.117	−0.038
28	0.330	0.009	0.151	−0.029	−0.020
29	0.054	−0.009	0.197	0.044	0.034
30	0.185	0.003	0.124	0.026	−0.011

TABLE XXI

SUMMARY OF INTRA-INFLORESCENCE CORRELATION COEFFICIENTS

	Ovules and ovules		Seeds and seeds		Length and length		Length and ovules		Length and seeds	
	f	Average	f	Average	f	Average	f	Average	f	Average
Positive...	19	+0.149	12	+0.031	16	+0.146	14	+0.077	10	+0.062
Negative..	1	−0.026	8	−0.022	4	−0.023	6	−0.133	10	−0.037
Total...	20	+0.140	20	+0.010	20	+0.112	20	+0.014	20	+0.025

appear in table XX, and these are still further summarized in table XXI.

The intra-inflorescence correlation for ovules is unquestionably positive, and perhaps high enough that one safely can say that the inflorescences are differentiated among themselves with respect to number of ovules produced. For number of seeds per locule the inflorescences seem not at all differentiated; it is not even possible to ascertain the sign of $r_{s's''}$, and its mean is only 0.010. This result seems to me of considerable physiological interest. I had expected to find a greater similarity among the numbers of seeds developing in the locules of the inflorescence than among the numbers of ovules formed. I thought that probably some inflorescences would be in much more advantageous positions for obtaining food material than others, and that in consequence the differences between inflorescences would be greater (and consequently the intra-inflorescence correlation higher) than for number of ovules. So far as we can judge from evidence at hand, the morphogenetic factor is stronger than the physiological[9] in determining the characteristics of the fruits of an inflorescence. For length, it seems reasonably certain that there is a slight similarity between the pods

[9] One must use extreme caution in such fields as this, for there are innumerable pitfalls. By morphogenetic I mean the organogenetic processes which give rise to the ovaries. By physiological factors I refer to (*a*) the ecological factors which determine whether an ovule shall receive a sperm, (*b*) to the availability of food material and other requisites for growth, (*c*) the innate vigor of the individual inflorescences which determine whether a fertilized ovule shall develop into a seed. The third of these is probably in some measure identical with the organogenetic. If (*a*) and (*b*) were really very different for the several inflorescences of an individual, one would expect the intra-inflorescence correlation for number of seeds to have sensible values and possibly to rise considerably above what it is for ovules. This is the case in *Sanguinaria* (Biometrika 7:328. 1910), where it seems that the main bulk of the

of the same inflorescence as compared with those of the tree in general.

Finally, the results from the two correlations fundamental to our present purposes are unmistakable. The evenness of the division between positive and negative and the extremely low mean value of the coefficients $r_{l'o''}=0.014$ and $r_{l's''}=0.025$ prove that there is no material relationship between the length of one pod and the number of ovules or seeds in another pod of the same inflorescence. This seems to me to prove conclusively that there are no differences in the supply of plastic materials of the different inflorescences sufficient to account for both the number of seeds developing and the length of an individual fruit deviating from their means in the same way.

For *Cercis* I have no data for the mature inflorescence comparable with that for *Staphylea*. It is interesting, however, to compare the intra-inflorescence correlations for number of ovules in the ovaries collected at flowering time in the spring of 1907 with the results obtained for *Staphylea*. The data for $r_{o'o''}$ are given in table XXII.[10] The correlations are

Tree 1, $r=0.571\pm0.015$
Tree 2, $r=0.213\pm0.020$
Tree 3, $r=0.378\pm0.021$

Mean, $r=0.388$

These results indicate a differentiation among the inflorescences of an individual of *Cercis* somewhat higher than we have found in *Staphylea*, but three individuals are not sufficient for more than a suggestion. The finding of an intra-inflorescence correlation in another genus gives confidence in the results for *Staphylea*. Should

correlation between the placentae of the fruit is due to ecological and physiological factors. There, however, we were dealing with individuals subjected to an external environment, not with the several inflorescences of the same individual. Possibly (*a*) and (*b*) are optimum for all inflorescences, but only a small percentage of the seeds develop because of some internal limiting factor. The bladdery fruits are possibly adaptive, and too great a weight of seed would offset the advantage of the peculiar structural features.

[10] Calculations by method described in Amer. Nat., 1910, The "ovules of first ovary" gives the grade, and the "number of associated ovaries" gives the frequencies for both variables, the tables being symmetrical.

TABLE XXII, CERCIS

Ovules of first ovary	Tree 1		Tree 2		Tree 3	
	Number of associated ovaries	Total ovules in associated ovaries	Number of associated ovaries	Total ovules in associated ovaries	Number of associated ovaries	Total ovules in associated ovaries
0	....	....	11	56	....	....
1	....	....	11	61	....	....
2	....	....	55	294	65	319
3	....	....	348	1891	168	854
4	21	163	1874	10096	1346	6594
5	7	55	3466	18422	2309	11330
6	409	3142	4600	24593	1358	6806
7	2322	17696	1118	6130	98	494
8	3984	30520	53	298	....	....
9	626	4813	....	....	....	....
10	27	214	....	....	....	....
Totals	7396	56603	11536	61841	5344	26397

an intra-inflorescence correlation for number of seeds and for length of pod be sometime demonstrated for matured fruits of *Cercis*, it would indicate that in this species a somewhat lower proportion of r_{ls} is due to a direct physiological relationship between the two characters than is indicated by the constants already calculated.

5. THE HYPOTHESIS OF THE DIFFERENTIATION OF INDIVIDUALS

If a sample of pods be made up of collections from a series of individuals, a (statistical) correlation will be found between two characters of the pod, say length and number of seeds, whether there is any physiological relationship or not, providing that the individuals are differentiated among themselves with respect to both of the characters in such a way that in the several individuals of the series both characters of the pair tend to fall above or below the means for all the individuals. Concretely, we understand for our present material that if, because of innate vigor or by reason of favorable environment, some individuals bore both larger pods and more seeds than the average, while other individuals with less innate vigor or with less favorable environment produced both smaller pods and fewer seeds than the average, then the correlation table prepared for the whole series of pods would show a sensible

interdependence for length and seeds which would not be due to any direct physiological relationship at all, but solely to differentiation in the plants which produced them.

The criticism that the correlations for pod characters may be due to heterogeneity of material has already been met for the present study, by analyzing the data from each individual independently. To make assurance doubly sure, we may determine the correlations (*a*) between the mean length of the fruit and the mean number of ovules per locule (r_{lo}), and (*b*) between the mean length of the fruit and the mean number of seeds per locule (r_{ls}), for the individual trees. Working by the brute force method we get

	1906	1907
r_{lo}	$=0.004\pm0.150$	0.010 ± 0.168
r_{ls}	$=0.418\pm0.124$	-0.371 ± 0.145

In both years r_{lo} is only a fraction of its probable error, and no significance whatever can be given it. Statistically, r_{ls} may be significant in both cases; for in 1906 $r/E_r=3.36$, and in 1907 $r/E_r=2.55$. Biologically the two constants, of roughly the same numerical order but opposite in sign, mean nothing except that mean length and mean seeds do not seem to be closely related. Probably both are determined by largely independent causes. The substantial quantitative results are due solely to the probable errors of sampling.[11]

[11] Reconsider in the light of these results the peculiar condition noted in table V, where it appeared that both r_{lo} and r_{ls} are lower for the population than for the mean values of these constants for the samples from individual trees. The explanation seems to be quite simple. The magnitude of r depends upon the largeness of the denominator, $\sigma_l\sigma_o$ or $\sigma_l\sigma_s$, as well as upon the numerator, S(lo) or S(ls), of the correlation formula. The mean $\sigma_{ls}\sigma_{os}\sigma_s$ of the individuals are seen in table V to be much lower than the same constants for the population. For both series the correlation between A_l and A_o is insignificant, and consequently we see a low value for r_{lo} for the population because of the high value of $\sigma_l\sigma_o$. This is also the tendency for r_{ls}, but in this case, the inter-individual correlation for A_l and A_s have material values which, although without biological significance because of their high probable errors, nevertheless have their influence upon the correlation constants for the population. In 1906, the inter-individual correlation is positive, and this tends to raise the population constant to about the same value as that for the mean of individuals, that is, 0.352 as compared with 0.387; but for 1907, the inter-individual correlation for means is negative and we find the discrepancy of 0.202 against 0.364. These results emphasize the importance of a stringently analytical treatment of data.

6. OTHER HYPOTHESES

The foregoing hypotheses have seemed the most reasonable ones to explain the relationship between the length of the fruit and the number of seeds developing, without the assumption of a direct causal relationship between them. All have given negative results in the sense that they have failed to show any reason for the interrelationship between length and number of seeds external to the two characters themselves. This does not prove that there is a direct causal relationship between them, that is, that their interdependence is not due to some outside influence, but I think that the factors suggested are the most important ones, and I have no data for taking up others on the present material.

We may conclude, therefore, with reasonable confidence, that the developing seed does in some way exert a developmental stimulus on the ovary wall. The nature of this stimulus must be ascertained by further studies.

V. Recapitulation

The chief problems, methods of reasoning, and conclusions from observations detailed both above and in an earlier paper on *Cercis*, may be briefly reviewed here.

That pollination is in many cases a stimulus to the development of the ovary now seems fairly well established. Several biologists have suggested that the developing seed also exerts an influence upon the growth of the fruit.

The establishment of this second hypothesis presents far greater difficulties than that of the first. So far as I am aware, no one has isolated bodies from the growing seed which when introduced into other ovaries accelerates development. Nor has it been proved that young ovaries with larger numbers of developing seeds show a higher rate of growth; and even if this were demonstrated, it would be impossible to say that the acceleration of growth was not due to the stimulation of an unusually large number of pollen tubes.

The most feasible method for a preliminary study seems to be to work with mature fruits and to ascertain whether the number of seeds may have had an influence in determining the size of the

fruit. If the size of the fruit increases as the number of seeds becomes larger, the development of the seed must exert a stimulus to the development of the fruit wall, providing that the correlation between the number of seeds and the size of the fruit is not due to some other factor or factors upon which both seed number and fruit size are in some degree dependent.

The task is, therefore, twofold: (*a*) to obtain a measure of the correlation between the number of seeds and the length of the fruit, and (*b*) to show by a process of elimination that the correlation can, with a high degree of probability, be attributed to a direct physiological relationship between number of seeds and size of fruit.

I. The first of these undertakings is straightforward. The coefficients of correlation show that in both *Cercis* and *Staphylea* there is a very substantial interdependence between number of seeds and fruit length.

II. The second task is somewhat more complicated. The following facts indicate that this observed interdependence is due to physiological factors confined to the seed and ovary wall:

(1) In *Staphylea* the correlation between the total number of seeds and the length of the fruit is higher than that between the number per locule and length.

(2) The relationship between the number of seeds developing and the length of the pod is in large measure independent of the influence of the number of ovules.

(3) In both *Cercis* and *Staphylea* the possibility of a mechanical stretching of the fruit through the pressure of adjoining seeds seems to be excluded.

(4) Both length of pod and number of seeds developing are slightly correlated with the number of fruits per inflorescence and with the distance of the node from the base of the inflorescence, but the correlations are too low to be of any significance in producing the relationship between the number of seeds and length of pod.

(5) The inflorescences of a shrub of *Staphylea* seem to be slightly differentiated with respect to the number of ovules per locule and the length attained by the fruit. Apparently the inflorescences

are not at all individual in the number of seeds developing per locule in the fruits which they produce. The cross correlation coefficients for the number of seeds in one fruit and the length of another fruit of an inflorescence furnishes no indication that there are innate or environmental peculiarities of inflorescences which tend to influence both the number of seeds developing and the length of the fruit in the same direction. In short, one cannot explain the correlation between number of seeds and length as the result of superior innate vigor or favorable nutrition in some inflorescences of an individual and the contrary conditions in others.

III. From the immediately foregoing considerations, and from others detailed in the body of the paper, we seem to be justified in the conclusion that the measurable interdependence between the number of seeds and the length of the fruit in *Staphylea* and probably also in *Cercis* is a direct physiological one, and that the two characters stand in some degree in the relationship to each other of cause and effect.

While this conclusion has already been reached by some other biologists depending upon more general evidence, I believe that this and the preceding study are the first in which a fairly satisfactory approximation to proof has been attained. A chief value of these studies is that the numerous difficulties surrounding the problem have been more clearly realized than appears to have been done before. The numerical results, while substantiating in a satisfactory manner the conclusions drawn from them, must be looked upon as merely approximations.

CARNEGIE STATION FOR EXPERIMENTAL EVOLUTION
COLD SPRING HARBOR, N.Y.

THE VEGETATION OF SKOKIE MARSH, WITH SPECIAL REFERENCE TO SUBTERRANEAN ORGANS AND THEIR INTERRELATIONSHIPS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 155

EARL E. SHERFF

(WITH TEN FIGURES)

The work on which this paper is based was begun in the autumn of 1910 and was concluded in the autumn of 1911. The detailed study of subterranean organs was carried on chiefly in the summer of 1911. The writer gratefully acknowledges his indebtedness for many valuable suggestions and much helpful advice, to Dr. HENRY C. COWLES and to Mr. GEORGE D. FULLER, under whose joint supervision the investigation was pursued, and also to Dr. J. M. GREENMAN for certain taxonomic assistance.

Skokie Marsh[1] is intimately associated with Skokie Stream, a small, sluggish stream beginning west of Waukegan, Ill., and extending southeast to a point west of Glencoe, Ill. Because of interference by cultivation and by drainage, the areal limits of the marsh can be defined only arbitrarily. As shown in the accompanying map (fig. 1), however, Skokie Marsh is approximately 12 km. long and at its southern end becomes 1.5 km. wide.

In early postglacial times, the marsh was an embayment (ATWOOD and GOLDTHWAIT **1**, p. 58), which later subsided, giving place to a system of drainage. At present the surface soil almost throughout the marsh consists of a black muck or partially decayed peat, 1 m. or less in thickness. Underneath is a subsoil of glacial clay.

General features of the marsh vegetation

Upon analysis, the vegetation at Skokie Marsh is found to consist of three rather pronounced formations.[2] Along the course

[1] For many additional data and photographs of Skokie Marsh, see BAKER (2).

[2] The words "formation" and "association" are used throughout this paper in the sense accepted by WARMING (16).

taken by Skokie Stream, the plants constitute distinctly a reed swamp formation (fig. 2). Extending along on either side of the reed swamp is a broad level expanse, intermediate between reed swamp and meadow. This may be designated swamp meadow (fig. 3). At the outer edges of the swamp meadow, in narrow areas that have not been too much disturbed by cultivation, true meadow

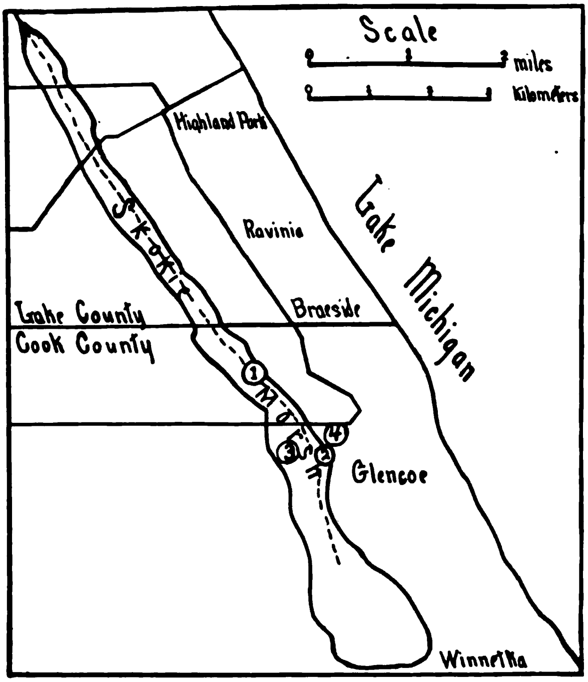


FIG. 1.—Map of Skokie Marsh; the dotted line represents Skokie Stream

is commonly present. At certain places, however, there is an abrupt transition from swamp meadow to forest.

In the reed swamp the plants belong to five easily recognized associations. Where the stream is deepest (as in fig. 2), aquatic or amphibious species, such as *Myriophyllum humile*,[3] *Ranunculus delphinifolius*, and *Potamogeton* (*zosteraefolius?*), are common near the center. In the shallower parts, the species are supple-

[3] All plant names given in this paper conform with the nomenclature of GRAY'S Manual, 7th ed., 1908.

mented or replaced by *Polygonum Muhlenbergii*, *P. hydropiperoides*, *Veronica Anagallis-aquatica*, *Radicula aquatica*, *Sium cicutaefolium*, *Sparganium eurycarpum*, *Glyceria septentrionalis*, *Alisma Plantago-aquatica*, *Rumex verticillatus*, *Callitriche heterophylla*, and *C. palustris*. As *Polygonum hydropiperoides* and *Sium cicutaefolium* are among the most abundant stream plants and appear to be dominant, we may classify the plants growing in the stream or upon its bed, except along the margins, as the *Sium-Polygonum* association; using SCHOUW's method of nomenclature (SCHOUW 14, pp. 148–150), we shall call this the *Sio-polygonetum*. On either side of the Sio-polygonetum a narrow or sometimes broad girdle[4] of *Nymphaea advena* and *Castalia odorata* occurs in many places along the stream. Usually these species are accompanied by species characteristic of the Sio-polygonetum; but the soil and light conditions present in

[4] The word "girdle" is here equivalent to the "zones" of many recent authors, and conforms with the recent proposal of FLAHAULT and SCHRÖTER (5), except that it is here used for "bands" that are not "concentric."

the girdles of *Nymphaea* and *Castalia* are peculiar to them and justify their treatment as a separate association, the *Nymphaeetum*. Landward from the Nymphaeetum are found dense and either intermixed or almost pure growths of *Typha latifolia*, *Sparganium eurycarpum*, *Scirpus fluviatilis*, and *S. validus*. Scattered to a varying extent among these species are *Sagittaria latifolia* and *Sium cicutaefolium*. Here and there are a few isolated patches of *Dulichium arundinaceum* and of *Decodon verticillatus*. This

FIG. 3.—Skokie Stream at point west of Glencoe, looking south; July

association will be referred to as the *Scirpo-typhetum*. Then again, in certain parts of the reed swamp, at stations slightly less hydrophytic, *Phragmites communis* is prominent. It forms exceedingly compact, nearly pure colonies that may reasonably be treated as an association, the *Phragmitetum*. Finally, we must mention the many large but somewhat scattered patches of *Iris versicolor* and *Acorus Calamus*, occurring in the outer parts of the reed swamp and often extending into the swamp meadow formation. These constitute an association of a very definite stamp, the *Iridoacoretum*.

A general comparison of the reed swamp associations shows that in the Sio-polygonetum and Nymphaeetum, where hydrophytism is greatest, the dominant plants are dicotyledonous. In fact, of the 15 species found to any appreciable extent in these two associations, the 10 most abundant (*Sium*, *Polygonum hydropiperoides*, *P. Muhlenbergii*, *Nymphaea*, *Castalia*, *Rumex*, *Veronica*, *Myriophyllum*, *Callitriche palustris*, and *C. heterophylla*) are dicotyledons.[5] In the other three associations the most abundant species are chiefly monocotyledons.

The swamp meadow differs from the reed swamp in being more uniform, due to greater parallelism between the water table and the soil surface, and does not admit of logical subdivision into associations. The plants are principally such grasses as *Calamagrostis canadensis*, *Glyceria nervata*, *Phalaris arundinacea*, *Poa triflora*, *Sphenopholis pallens*, and *Agrostis perennans*. These are frequently interspersed with *Carex lupuliformis*, *C. vesicaria monile*, *Scirpus atrovirens*, and *S. Eriophorum*. The swamp meadow is used by farmers of the district for the production of marsh hay, and many of them customarily burn over the areas in late autumn. Most of the shrubs and young trees are killed in this way, and so forest development is hindered. Trees occur only in small groups, consisting chiefly of *Salix* (*S. nigra* and other species), *Fraxinus americana*, and *Populus tremuloides*. Frequently associated with these are such shrubs as *Cornus stolonifera*, *Cephalanthus occidentalis*, and *Sambucus canadensis*.

Throughout the reed swamp and swamp meadow are many species which, though very abundant, share only to a small extent in giving to the several associations their distinctive appearance. Thus, *Ludwigia palustris*, *Proserpinaca palustris*, *Penthorum sedoides*, and *Stenophyllus capillaris* are low in habit and obscured by taller plants in the shade of which they may thrive. Again, *Aster Tradescanti*, *Boltonia asteroides*, *Lobelia cardinalis*, *Teucrium occidentale*, and *Scutellaria galericulata*, while extremely common, are nevertheless conspicuous only during the latter part of the summer. The names of such species will be given in this paper only where occasion demands.

[5] See HENSLOW (7), however, regarding the supposed monocotyledonous nature of *Nymphaea* and *Castalia*.

The meadow formation, as already stated, is narrow and more or less interrupted. The soil surface slopes mildly upward, away from that of the swamp meadow. The vegetation is much diversified at different places and from month to month during the vegetative season. *Poa pratensis* and *Agrostis alba* are the dominant grasses, but *Danthonia spicata* and *Agropyron caninum* are frequent. Scattered among the grasses are *Carex stipata*, *C. vulpinoidea*, *C. scoparia*, and *Eleocharis palustris*. In some parts of the meadow *Viola cucullata*, *Senecio aureus*, and *S. Balsamitae* are conspicuous in May and June, while later such species as *Lilium canadense* and *Rudbeckia hirta* are the most noticeable.

In the entire marsh there were found, exclusive of shrubs and trees, 163 species of pteridophytes and spermatophytes. Of these, 68 were common or even abundant.

Certain ecological factors

Four Livingston atmometers were set out May 21, 1911, at different stations indicated in fig. 1. Readings were taken weekly from May 21 to October 15, and afterward corrected according to the method outlined by LIVINGSTON (**9**, p. 273, and **11**).[6] A detailed account of the evaporation data thus obtained may be published subsequently elsewhere, but only the general results will be given here. It was found that the average daily evaporation at station 1 (in the center of the reed swamp) for the 147 days was 3 cc.; at station 2 (in the outer part of the reed swamp), 4.5 cc.; at station 3 (in the swamp meadow), 4.27 cc.; and at station 4 (in a stretch of forest running along the east side of the marsh and composed chiefly of *Quercus bicolor* and *Fraxinus americana*), 7.91 cc. Thus it will be seen that the evaporation rate was lowest in the reed swamp; that the evaporation rates in the reed swamp and the swamp meadow were closely similar; and that these rates were from about 38 per cent to about 57 per cent as great as the rate in a neighboring forest of *Quercus bicolor* and *Fraxinus americana*.

[6] The unglazed portion of each cup was placed at a mean height of 2.5 dm. above the soil surface. The instruments were not provided with a rain-excluding device, such as that recommended by LIVINGSTON (**10**).

From September 3 to October 22, 1911, weekly readings were taken of the rates of evaporation at different levels above the soil surface. Among the plants of *Phragmites*, four atmometers were placed at levels ranging from 0 m. to 1.95 m. above the soil. The average daily rate for the seven weeks at 1.95 m., or near the top of the *Phragmites* plants, was found to be 7.5 cc., just three times as great as the average daily rate of 2.5 cc., at the surface of the soil. Similar results were obtained with five atmometers in a dense growth of *Typha*. In each case the data secured are found to support YAPP's important contention (**20**) that for species growing side by side, but vegetating mainly at different heights, the conditions of growth may be very unlike.

The depth of the water table in the reed swamp and the swamp meadow was observed each week from May 21 to October 22, 1911. The water in Skokie Stream was about 1 m. deep in May; its depth then gradually decreased until in July, when the stream bed was in most places fairly dry; in August the water began to rise again, and by October had reached an average depth of about 1.1 m. In the rest of the reed swamp and in the swamp meadow the water table during May was coincident with or above the soil surface; in early September it sank to the maximum depth of 1 m. in the reed swamp and 1.75 m. in the swamp meadow; and then, rising rapidly, reached the surface again by the middle of October. According to farmers in the vicinity of Glencoe, Skokie Stream has sometimes in the past risen until a depth of about 3 m. was reached; in such cases the entire marsh was of course deeply submerged. Various attempts have been made to classify the constituent species of a formation with relation to the optimum water table depth for each species. But where the water table varies greatly in depth from month to month and from year to year, data must be secured through many years if they are to show more than merely the relative degrees of hydrophytism to which plants in different places are subject.

Litmus tests each week, from May 21 to October 22, 1911, showed the water in Skokie Stream to be either neutral or slightly alkaline. Similar tests showed the soil water in the outer parts of the reed swamp and in the swamp meadow to be usually neutral or slightly

alkaline; only for a few days in August was acid present, and then the amount was almost negligible.

Subterranean organs and their interrelationships

A study of the subterranean organs of the reed swamp plants showed that in many cases the depth is roughly proportionate to the depth of the water table. YAPP (19) arrived at a similar conclusion concerning the plants at Wicken Fen. And since the depth of the water table may influence the depth of the subterranean

FIG. 4.—*a*, *Sparganium eurycarpum*; *b*, *Sagittaria latifolia*; *c*, *Polygonum Muhlenbergii*; July.

organs, the latter in turn may enter as a potent factor into the success or failure of various species. Thus, for example, the rhizomes of *Polygonum Muhlenbergii*, where this species occurs in the Sio-polygonetum, are usually at or near the surface of the stream bed. As KING (8, p. 240) and others have pointed out, saturated soil like that of the stream bed does not admit oxygen freely. And so, in the Sio-polygonetum, the rhizomes of *Polygonum* and their roots appear advantageously placed. But in the Scirpo-typhetum (fig. 4), where the surface soil is occupied by an extremely dense mat composed of the rhizomes of *Typha*, *Sparganium*, and

Scirpus, the rhizomes of *Polygonum* average about 10 cm. in depth. Hence in the Scirpo-typhetum, although the rhizomes of *Polygonum* are lower, evidently, in response to the greater average depth of the water table, they gain the additional advantage of being able to travel with less interference from the other rhizome systems.

An examination of *Typha*, *Sparganium*, *Scirpus fluviatilis*, and *S. validus* shows these species to be very similar in growth-form and hence capable of keen competition. Where any one of these species becomes more abundant in the Scirpo-typhetum, the others become less so. Because of the thick, strong rhizomes, the subterranean competition is to some extent mechanical; but, as CLEMENTS (**3**, pp. 285–289) maintains, it is probably to a much greater extent physiological (or "physical"), especially in the case of the roots proper. The opposition that any or all of these species can offer to the intrusion of other species makes their hold upon the soil very effective. With *Sagittaria* (fig. 4), however, the case is different. Its growth-form favors a less compact arrangement of the individual plants. Its rhizomes cannot produce a thick mat. Obviously, as the plants of *Sagittaria* are developing vegetatively, other species, such as *Typha*, *Sparganium*, and *Scirpus*, may easily invade and occupy the soil with their densely matting rhizomes. Subsequently the rhizomes of *Sagittaria*, if they are to establish new plants at proper distances away from the parent plant, must either plough their way along through the surface mat of rhizomes or travel underneath. They usually do the latter. As a rule several rhizomes start growth from each plant in early summer, in a downward direction; at a depth of 10–15 cm. they assume a horizontal direction for some distance; they then grow upward again, with a tuberous, propagative thickening near the distal end, and finally resemble somewhat a shallow, inverted arch.[7] Thus interference from surface rhizomes and roots is to a great extent avoided. In this case, then, while it is not certain that the inverted arch of the *Sagittaria* rhizome is a direct adaptation to this particular struggle, it is certain that the inverted arch, however induced originally, is here of the greatest value.

[7] For illustrations of the similar rhizomes of *Sagittaria sagittifolia* see GLÜCK (**6**, *pl. 6* and *figs. 35* and *39*).

PIETERS (13) found among the plants of western Lake Erie that even where *Sagittaria latifolia* was most abundant, *Sparganium* (and *Zizania*) had secured a foothold. On the other hand, throughout all the broad "zones" of *Sparganium*, *Scirpus validus* ("*S. lacustris*"), and *S. fluviatilis* that he describes, he says *Sagittaria latifolia* was common.

A study of the subterranean organs of *Sagittaria*, *Sparganium* (or *Typha* or *Scirpus*), and *Polygonum* shows that because of differences in direction or in depth they conflict but little. Again, because of differences in growth-form, their aerial parts do not conflict seriously. Thus a given area can usually support a greater mass of vegetation if these three growth-forms be present in fair mixture than if only one be present. SPALDING (15) has described the mutual relationships of *Cereus giganteus* and *Parkinsonia microphylla*, two desert species which thrive together because the occupation of different depths by their root systems enables them "to utilize to the utmost the scanty rainfall." WOODHEAD (18) found *Holcus*, *Pteris*, and *Scilla* forming a non-combative "society or sub-association." For a group of plants mutually competitive, WOODHEAD uses the term "competitive association." Recently WILSON (17) likewise speaks of a "complementary association" or "society." But the use of the words "association" and "society" in this connection is unfortunate. These words have already been used by COWLES (4) and others (see WARMING **16**, p. 144) to denote a primary subdivision of a formation. As will be seen later (and in fact as WOODHEAD's use interchangeably of "sub-association" and "association" would imply), not all complementary or competitive groups are coextensive with a true association. We shall here substitute the word community, which is of less restricted application. Thus, *Sagittaria* and *Polygonum*, where occurring in the Scirpo-typhetum with either *Typha* or *Scirpus fluviatilis* or *S. validus*, constitute a complementary community. But *Sparganium*, *Typha*, *Scirpus fluviatilis*, and *S. validus*, where they occur intermixed, form a competitive community.

Species that are complementary in one association may be less so in another. Thus, *Polygonum Muhlenbergii* and *Sparganium* are complementary in the Scirpo-typhetum; but in the Sio-

polygonetum, where their rhizomes lie in common near or at the surface of the stream bed, they are "edaphically" (see WOODHEAD **18**) competitive, and hence complementary only in an aerial way. In this particular case, however, the frequently open appearance of the vegetation in the Sio-polygonetum indicates that the mutual biotic struggle of the two species is less keen than their separate struggles against somewhat adverse environmental conditions.

In the reed swamp certain mints become conspicuous during midsummer, particularly so in the Scirpo-typhetum, where they thrive in the shelter of *Typha* and other tall plants. *Teucrium occidentale* and *Scutellaria galericulata* are very common. They produce from their basal nodes numerous slender stolons that run out at different depths in the soil, and these stolons may produce new plants. These species tend to have their root systems 3–6 cm. lower in wet situations than in dry, although exceptions to this rule are not rare. But whether growing from plants in dry or from those in wet situations, the new stolons exhibit a remarkable power of changing their direction of growth, in response to numerous obstructions, and thus they may proceed further without serious results. Considering the strength and size of the rhizomes of *Typha*, *Sparganium*, and *Scirpus*, also the delicate nature of the stolons of *Teucrium* and *Scutellaria* and their capacity for altering growth-direction, it is probable that mechanical competition between such rhizomes as those of *Typha* and such stolons as those of *Teucrium* is practically absent. Again, the aerial parts of the *Typha* form vegetate chiefly in higher atmospheric strata than do those of the *Teucrium* form. Evaporation readings show that in the higher strata evaporation is much greater. And while plants of relatively xerophytic structure (e.g., *Typha*, *Sparganium*, and *Scirpus*) are fitted to withstand acute drying conditions, plants with foliage of looser texture (e.g., *Teucrium* and *Scutellaria*) can vegetate better in lower strata where the effect is that of greater humidity; the abundance of the latter plants among the former at Skokie Marsh tends to confirm this statement. Further, the persistence with which tall plants like *Typha* become dominant under favorable soil conditions shows that they are not, at least noticeably, harmed by plants like *Teucrium*. If, finally, we allow for the great avail-

ability of nitrogenous foods in the soil and for the differences in food requirements, it becomes clear that the numerous communities of *Typha* and *Teucrium*, *Typha* and *Scutellaria*, *Sparganium* and *Teucrium*, etc., are complementary.

The purity of the Phragmitetum has already been mentioned. Many species that flourish elsewhere in the reed swamp under a wide range of light, moisture, and other shelter conditions fail to thrive here. Only *Calamagrostis canadensis* gains noticeable

FIG. 5.—*Phragmites communis;* July

entrance, and then imperfectly. The dead *Phragmites'* growth of previous years makes a considerable but loose covering near the soil, its decay not being facilitated as in the Scirpo-typhetum, where water is more abundant. This dead cover may perhaps act as a partial check upon the invasion of other species. But a study of the rhizomes of *Phragmites* (fig. 5) shows another fact which probably is more important. They do not occupy one particular level, but rather several different levels of soil. As a result, there is formed a dense mat of rhizomes and roots, about 2.5 dm. deep. Obviously, the subterranean organs of other species which might

start growth here must compete with the extraordinarily large number of *Phragmites* roots and rhizomes. Where other factors are suited equally to *Phragmites* and to competing species, this biotic factor in the subaerial struggle ought usually to decide in favor of *Phragmites*.

The Nymphaeetum displays many complementary communities. The rhizomes of *Nymphaea advena* (fig. 6) are usually

FIG. 6.—*a*, *Ranunculus delphinifolius*; *b*, *Nymphaea advena*; *c*, *Sium cicutaefolium*; *d*, *Typha latifolia*; *e*, *Polygonum hydropiperoides*; drawn in early July.

5–10 cm. thick and lie mostly at a depth of 8–25 cm. below the soil surface. The rhizomes of *Castalia odorata*, while smaller, lie at a similar depth. Where the Nymphaeetum intergrades with the Scirpo-typhetum, as is commonly the case, the rhizomes of *Typha*, *Sparganium*, and *Scirpus validus* lie higher in the soil. In many places the soil surface itself is occupied by the stolons of *Ranunculus delphinifolius* and the creeping stems of *Polygonum hydropiperoides*, with a large, upright stem base of *Sium cicutaefolium* present here

and there. In other places, *Ranunculus* is replaced by *Myriophyllum humile* or by young plants (growing chiefly from detached leaves) of *Radicula aquatica*, while *Polygonum* is replaced by *Veronica Anagallis-aquatica*, and *Sium* by *Rumex verticillatus*. And while it is true that *Nymphaea* and *Castalia*, or *Typha* and *Sparganium* and *Scirpus*, or *Ranunculus* and *Myriophyllum* and *Radicula*, or *Polygonum* and *Veronica*, or *Sium* and *Rumex* are mutually competitive, yet a complete community (as shown, e.g., in fig. 6) is complementary; the basal parts chiefly because of different depths, and the upper parts chiefly because of different growth-forms.

An inspection of the Nymphaeetum shows that only where *Nymphaea* is nearly or quite absent does *Sagittaria latifolia* successfully invade from the Scirpo-typhetum. As is commonly known, the rhizomes of *Nymphaea* in many habitats are usually decayed to within a short distance of the growing apex. An investigation during August 1911 showed that generally where the rhizomes of *Sagittaria* had penetrated these decayed parts, they themselves had started to decay.[8] Frequent cases were found where the decayed *Nymphaea* rhizomes lay nearer the surface and the *Sagittaria* rhizomes had proceeded underneath, unharmed. Speaking in a general way, while *Nymphaea* and *Sagittaria* thrive better in the Nymphaeetum and Scirpo-typhetum respectively, yet along the line of tension between these two associations the injury done by the decayed *Nymphaea* rhizomes to the rhizomes of *Sagittaria* is a factor that appears to be decisively in favor of *Nymphaea*. The inverted rhizome arch of *Sagittaria*, useful in the Scirpo-typhetum, is here more often harmful.

In many parts of the Irido-acoretum, *Polygonum Muhlenbergii* and *Galium Claytoni* abound, and these form with *Acorus* a complementary community (fig. 7). The creeping stems of *Galium* root upon the soil surface, the rhizomes of *Acorus* lie just beneath, and those of *Polygonum* are deepest of all. The bushy shoot of *Galium* appears not to harm the slender, ensiform leaves of *Acorus*, and

[8] Many litmus tests uniformly showed the decayed parts of the *Nymphaea* rhizomes to be strongly acid. Enough cultural experiments have not been performed, however, to determine whether the effect upon the *Sagittaria* rhizomes, as above noted, is due to acid or to other causes.

they in turn do little harm to it. In late summer, the shoots of *Polygonum* rise above those of *Acorus* and *Galium* without apparent harm to either of them. And while *Polygonum* might increase in abundance if *Acorus* and *Galium* were entirely absent, still to a great extent the community, viewed as a whole, is complementary. Elsewhere in the Irido-acoretum the rhizomes of *Acorus* are replaced by those of *Iris;* and very often the rhizomes of *Galium* are replaced by those of *Ludwigia palustris, L. polycarpa, Proserpinaca*

FIG. 7.—*a, Acorus Calamus; b, Polygonum Muhlenbergii; c, Galium Claytoni;* July

palustris, Penthorum sedoides, Veronica scutellata, or *Campanula aparinoides.*

The basal parts of the various swamp meadow species are usually more slender than those of the reed swamp species, and hence the texture of the surface mat of rhizomes, roots, etc., is finer. Then, too, reproduction by seeds becomes more common. *Polygonum Muhlenbergii* is present in the swamp meadow, and by means of its extensively creeping rhizomes, which lie rather low, it forms in some places large patches. Certain other perennials, e.g., *Asclepias incarnata* and *Sium cicutaefolium,* which root near the surface, may reproduce largely by seed or by new shoots arising from the old stem base of the preceding year. In the middle

and latter parts of the summer, when the surface soil is no longer saturated with water, such annuals as *Panicum capillare*, *Echinochloa Crus-galli*, *Eragrostis hypnoides*, *Stenophyllus capillaris*, *Polygonum Persicaria*, *Amaranthus paniculatus*, and *Erechthites hieracifolia* take possession of all exposed surface soil and become exceedingly abundant. Much of the surface soil that has been denuded by burning or by other causes is already occupied, however, by the rhizomes of perennials such as *Ludwigia palustris*, *L. polycarpa*, *Proserpinaca palustris*, etc. In these cases *Boltonia*

FIG. 8.—*a*, *Boltonia asteroides*; *b*, *Penthorum sedoides*; *c*, *Proserpinaca palustris*; *d*, *Ludwigia palustris*; *e*, *Callitriche palustris*; July.

asteroides, *Callitriche heterophylla*, and *C. palustris* are often abundant; both species of *Callitriche*, however, die away in midsummer, becoming replaced by annuals. Fig. 8 shows such a community. *Callitriche*, maturing earliest, is "seasonally" (WOODHEAD **18**) complementary with the other species. *Boltonia* roots lowest, while its aerial shoot grows much the highest; and since it is not harmed very much by *Proserpinaca*, *Ludwigia*, and *Penthorum*, while they derive, if anything, benefit from its shelter, *Boltonia* is complementary both aerially and subaerially. *Proserpinaca*,

tuber-bearing rhizomes of *Equisetum arvense*. In drier situations the bulbs of *Lilium canadense* occur at a similar depth (most often about 10 cm. deep). Higher in the soil may be found (fig. 9) roots of such species as *Asclepias incarnata*, *Thalictrum revolutum*, and *Lathyrus palustris*, while the surface soil contains a mixture of the root systems of *Poa pratensis*, *Agrostis alba*, *Eleocharis palustris*, *Acalypha virginica*, etc. In the community shown in fig. 9, *Equisetum* is edaphically complementary, but (considering only the aerial sterile shoots) aerially competitive with *Poa*, *Agrostis*, *Eleocharis*,

FIG. 10.—*a*, *Lycopus americanus*; *b*, *Viola conspersa*; *c*, *Viola cucullata*; *d*, *Iris versicolor*; July.

and *Acalypha*. To a moderate extent, the plants rooting near or at the surface appear to be complementary with the plants rooting deeper.

Small, apparently open depressions are numerous in the moist parts of the meadow. These generally contain (fig. 10) such plants as *Iris*, *Acorus*, *Viola conspersa*, *V. cucullata*, *Cardamine bulbosa*, and seedlings of *Lycopus americanus*. And while the rhizomes of *Cardamine* and *Lycopus* occur almost invariably just below those of the other species, and while the different species doubtless make

different demands upon the soil, yet edaphic competition is undoubtedly sharp. The almost complete absence, in these small areas, of stoloniferous or loosely spreading species makes it seem certain that there exists some mechanical competition in which species of compact and frequently caespitose habit or species capable of reproducing extensively from seed are successful. The extent, however, to which their success is achieved because of their growth-form or because of their superior adaptation to the particular complex of soil and moisture conditions in these small areas is of course incapable of accurate estimation without further study. The idea of mechanical competition (i.e., a struggle either among the various species because of the mutual bodily resistance of any or all of their growing parts, or of individual species because of the resistance offered by the soil's compactness to the locomotion of their subterranean organs) is opposed by CLEMENTS (**3**, pp. 285–289); but WARMING (**16**, p. 324), in accounting for the usual absence of vegetative locomotion among perennial herbs of the meadow formation, seems inclined to accept this idea in part.

Summary and conclusions

1. Atmometer readings, taken for seven weeks at four different levels among *Phragmites* plants and at five different levels among *Typha* plants, show that among marsh species of compact social growth evaporation is proportionate to the height above the soil. These results thus coincide with those of YAPP (**20**).

2. Data accumulated at Skokie Marsh appear to support the conclusion of MASSART (**12**) that it is a matter of importance to perennial plants that their hibernating organs occupy a definite level in the soil.

3. Certain observed cases of variation in this level (*Teucrium occidentale*, *Polygonum Muhlenbergii*, etc.), corresponding to changes in the water level, indicate that with certain species, at least, the depth of the water table is much the most potent controlling factor.

4. Two or more species may live together in harmony because (1) their subterranean stems may lie at different depths; (2) their roots may thus be produced at different depths; (3) even where roots are produced at the same depth, they may make unlike

demands upon the soil; (4) the aerial shoots may have unlike growth-forms; or because (5) even where these growth-forms are similar, they may vegetate chiefly at different times of the year. According as one or more of these conditions control the floristic composition of a given community the community may be called complementary.

5. The root depth having been determined by various factors for the different species in a community, the specifically different root systems then function in a complementary or a competitive manner as the case may be. But even if the root systems be complementary, the community may be competitive because of marked competition among the aerial parts. Likewise, competitive root systems may render competitive a community otherwise complementary.

6. Through the ability of certain species to utilize different strata in the soil, the aerial portions of these plants are brought into a closer competition. And with closer competition, the chances in the past for further adaptation of similar aerial shoots to dissimilar growth conditions must have been greatly increased. Hence communities, formerly complementary in a purely edaphic way, may have been largely instrumental in the evolution of completely complementary communities. In so far as they have been thus instrumental, the fact deserves great emphasis, especially when we consider the far-reaching changes in form and anatomical structure necessarily developed as a prerequisite to living in a completely complementary community.

LITERATURE CITED

1. Atwood, W. W., and Goldthwait, J. W., Physical geography of the Evanston-Waukegan region. Ill. State Geol. Surv. Bull. 7. 1908.
2. Baker, F. C., The ecology of the Skokie Marsh area, with special reference to the Mollusca. Bull. Ill. State Lab. Nat. Hist. 8: no. 4. 1910.
3. Clements, F. E., Research methods in ecology. 1905.
4. Cowles, H. C., The plant societies of Chicago and vicinity. Geog. Soc. Chicago. Bull. no. 2. 1901.
5. Flahault, Ch., and Schröter, C., Phytogeographic nomenclature. Intern. Congress Brussels. Circ. 6. pp. 28+x. 1910.

6. GLÜCK, H., Biologische Untersuchungen über Wasser- und Sumpfgewächse. Erster Teil. 1905.
7. HENSLOW, G., The origin of monocotyledons from dicotyledons, through self-adaptation to a moist or aquatic habit. Ann. Botany **25**:717–744. 1911.
8. KING, F. H., The soil. 1897.
9. LIVINGSTON, B. E., Evaporation and plant development. Plant World **10**:269–276. *fig. 1.* 1907.
10. ———, A rain-correcting atmometer for ecological instrumentation. Plant World **13**:79–82. *fig. 1.* 1910.
11. ———, Operation of the porous cup atmometer. Plant World **13**:111–119. 1910.
12. MASSART, J., Comment les plantes vivacés maintenent leur niveau souterrain. Bull. Jard. Bot. l'Etat Bruxelles **14**:113–142. *figs. 12.* 1903.
13. PIETERS, A. J., The plants of western Lake Erie, with observations on their distribution. U.S. Fish Commission Bull. **21**:57–79. *pls. 11–20.* 1901.
14. SCHOUW, J. F., Grundtraek til en almindelig Plante-geographie. 1822.
15. SPALDING, V. M., Problems of local distribution in arid regions. Amer. Nat. **43**:472–486. 1909.
16. WARMING, E., Oecology of plants. 1909.
17. WILSON, M., Plant distribution in the woods of N.E. Kent. I. Ann. Botany **25**:857–902. *pls. 3. figs. 4.* 1911.
18. WOODHEAD, T. W., Oecology of woodland plants in the neighborhood of Huddersfield. Jour. Linn. Soc. **37**:333–496. *figs. 70.* 1906.
19. YAPP, R. H., Sketches of vegetation at home and abroad. IV. Wicken Fen. New Phytol. **7**:61–81. *pls. 4. figs. 9–15.* 1908.
20. ———, On stratification in the vegetation of a marsh, and its relations to evaporation and temperature. Ann. Botany **23**:275–320. *pls. 20. figs. 8.* 1909.

BRIEFER ARTICLES

ABNORMALITIES IN PROTHALLIA OF PTERIS LONGIFOLIA

(WITH FOUR FIGURES)

Some abnormal conditions in archegonia were noted in prothallia, probably of *Pteris longifolia*. The spores had been sown about the middle of October, on moist sphagnum in a low jar covered with a glass plate. The resulting prothallia, after three weeks, were partly used in class work. Those remaining after class use were put aside for further development, in the hope of getting material for histological preparations. No particular care was taken to keep conditions constant or normal. The moisture varied greatly at times, and the temperature was a very variable factor, since for some time the jar was kept on the sill of a none too tight east window. As a result of some extremely cold weather, it was removed to a less exposed position on a shelf, somewhat darker than that on the window sill. In January the material was killed and fixed in 0.6 per cent chromacetic acid, washed, dehydrated, and imbedded in paraffin. The sections were cut 5 μ thick. Safranin and gentian violet were principally used in staining.

The prothallia were unusually small, and in sections the sex organs appeared smaller than is usual in *Pteris*. In spite of many normal archegonia, 8 cases were found in about 35 prothallia where there were more than two neck canal cells. In 5 of these, there were definitely and certainly four such nuclei, either arranged in a row, as in fig. 1, or grouped closely together near the mouth of the canal. In the other cases, the condition of the nuclei was such that it could not be ascertained whether the number was three or four. The four-nucleate neck canal cell has been reported for Filicineae by Miss TWISS[1] in *Lygodium circinatum*, where occasionally this condition occurs instead of the usual two neck canal nuclei.

A second abnormality which occurred in these prothallia is shown in fig. 2. Here there are evident two eggs, two ventral canal cells, and the usual two neck canal nuclei. This condition has been reported for

[1] TWISS, EDITH MINOT, The prothallia of *Aneimia* and *Lygodium*. BOT. GAZ. 49:168–181. *pls. 10, 11.* 1910.

Adiantum cuneatum by Miss LYON,[2] and again by Miss FERGUSON[3] in *Pteris*, probably *P. cristata*. Unlike the case cited by Miss FERGUSON, the basal cell did not give rise to the second egg and ventral canal cell, but had divided periclinally into approximately equal cells. In some other archegonia a similar periclinal division gave rise to two unequal cells, not strikingly different in proportions from an egg and ventral canal cell, but not having the characteristic granular appearance of such.

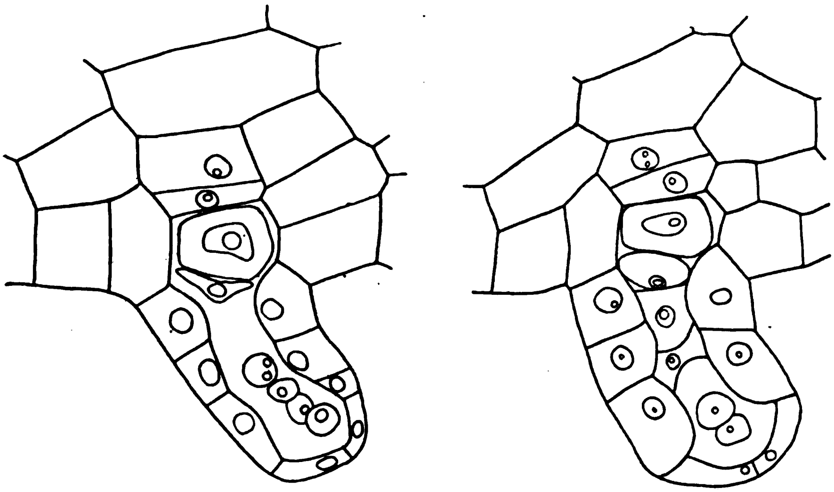


FIG. 1 FIG. 2

FIGS. 1, 2.—Fig. 1, archegonium of *Pteris longifolia*, showing four neck canal nuclei; ×500; fig. 2, archegonium in which two eggs and two ventral canal cells have been formed; the basal cell has divided periclinally; ×500.

A third unusual condition, of which no former report has come to hand, is one in which a definite wall has been formed between the two neck canal nuclei, giving two neck canal cells. This preparation is shown in fig. 3. The cells are practically equal in size and very similar, or one might be led to believe that this is an early stage in the development of such an archegonium as shown in fig. 2. In this archegonium the basal cell appeared to have divided unequally in a periclinal direction.

[2] LYON, FLORENCE M., Evolution of the sex organs. BOT. GAZ. 37:280–293. *figs. 16.* 1904.

[3] FERGUSON, MARGARET C., Imbedded sexual cells in the Polypodiaceae. BOT. GAZ. 51:443–448. *pls. 26, 27.* 1911.

Although sporophytes were rarely found in the material used, one appeared in which an entire quadrant, the foot, had failed to develop. In another prothallium, there was a structure which appeared to be an apogamous sporophyte.

An antheridium, in which the basal cell has apparently given rise to spermatogenous tissue, is shown in fig. 4. The cap cell and ring cells appear normal, except for an unusual slope of the walls. Unfortunately

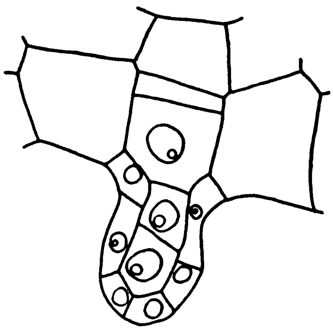


FIG. 3

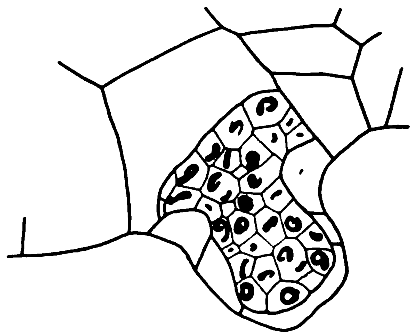


FIG. 4

FIGS. 3, 4.—Fig. 3, archegonium showing a definite wall between the two neck canal nuclei; ×500; fig. 4, antheridium in which the basal cell has given rise to spermatogenous tissue; ×500.

the section figured was the last on the slide, so that the structure could be traced in one direction only.

The writer is indebted to Professor JOHN M. COULTER and Dr. W. J. G. LAND for suggestions in this work, and also to Mr. LOREN C. PETRY, who kindly turned over his excellent preparations made from this material.—NORMA E. PFEIFFER, *The University of Chicago.*

SIR JOSEPH DALTON HOOKER

(WITH PORTRAIT)

The recent death of Sir JOSEPH DALTON HOOKER, at the advanced age of nearly 95 years, removes from the ranks of living botanists one of the most distinguished scientific men of our times; his long, continuous, and active career of over 70 years in the botanical field has been equaled by few men. JOSEPH DALTON HOOKER was born June 30, 1817, at Halesworth, Suffolk, England, and died December 10, 1911, at his home near London. The son of an eminent botanist, living in a scientific

atmosphere, it was but natural that his life work should be in botany rather than in the medical profession for which he was educated primarily, having taken the degree of M.D. at the University of Glasgow in 1839.

HOOKER'S botanical work began in his father's herbarium, and his early interests were mainly in the lower groups of plants, particularly the mosses. In 1837, at the age of 20, he published his first contribution to botanical literature. Two years later he was commissioned botanist to the Antarctic Expedition under the command of Sir JAMES CLARK ROSS, and in this capacity acquired in a comparatively short time an extensive knowledge of the floras of the south temperate and sub-antarctic regions; the results of this expedition were embodied in six large quarto volumes under the general title of *The botany of the Antarctic voyage of H.M. discovery ships Erebus and Terror in the years 1839–1843 under the command of Captain Sir James Clark Ross*, published 1844–1860. Although HOOKER had concerned himself chiefly with the lower groups of plants, yet he early developed an interest in fossil botany, and this interest was fostered by the appointment in 1845 to the position of botanist to the Geological Survey of Great Britain; he remained in the service of the survey for about two years and made important contributions to paleobotanical literature.

The desire for a more extended knowledge of the flora of the Old World tropics led HOOKER to organize a botanical expedition to India. The project received recognition and favor, and accordingly he entered this little known field in 1848. Some of the results of his early observations in India were published in *The Himalayan journals* and in a single volume under the title of *Flora Indica*, the latter work being collaborated with Dr. THOMAS THOMSON and issued in 1855. In this year HOOKER

was appointed assistant director of the Royal Botanic Gardens at Kew, a position which he held for ten years. It was a decade of extraordinary activity in botanical exploration and in the study of herbarium collections; and it was during this time that the preparation of a comprehensive and much needed work on the genera of plants was formulated, and happily the elaboration of the *Genera plantarum* was undertaken in collaboration with Mr. GEORGE BENTHAM, and a part of the first volume of this monumental work appeared in 1862.

Upon the death of Sir WILLIAM JACKSON HOOKER, the eminent director of the Kew Gardens, JOSEPH DALTON HOOKER succeeded to the directorship, and this post he most successfully occupied for about 20 years. During this time vast improvements were made at the Gardens, the collections at the Kew Herbarium were greatly augmented, important publications were completed, notably the *Genera plantarum*, and others were continued; but with all the onerous duties of this important office time was found for further botanical explorations in various parts of the world. In 1877 HOOKER visited the United States, and in company with Dr. ASA GRAY an expedition was made across the continent to California; the results of this journey were incorporated in a joint paper by GRAY and HOOKER which appeared in 1881.

In 1885 HOOKER retired from the directorship of Kew, but from that time until shortly before his death he continued actively but privately in independent taxonomic research. By far the greater amount of HOOKER's published work (and the number of titles exceeds 200) has been in floristics. Because of his comprehensive knowledge of botany and his broad conception, his productions have been masterly; but his constant interest in plant distribution and his numerous writings on this subject are of such a character as justly to give him the rank of an authority in this field. In fact it may be said that HOOKER was here at his best. His papers on the geographical distribution of plants are full of originality, the facts are marshaled in a logical and convincing order, and the subject-matter is written in an attractive style, so that his published papers are among our most suggestive and reliable sources of information in this department of botanical science.

The esteem and high regard in which Sir JOSEPH DALTON HOOKER, as a man and scientist, was held by his contemporaries is indicated by the many honors extended to him by numerous scientific societies and learned organizations both at home and abroad; in several of these he took an active part for the attainment and advancement of scientific knowledge.—J. M. GREENMAN, *Chicago*.

CURRENT LITERATURE

BOOK REVIEWS

Heredity

Several courses of public lectures on heredity have been made the basis of a very readable book by CASTLE,[1] in which the principles of Mendelian heredity and other related topics are discussed with special reference to their bearing upon evolution and animal breeding. The rapidly increasing number of expositions of Mendelism are warranted both by the growth of scientific knowledge, and by the popular demand for information, and it is gratifying to have the subject presented in easily comprehensible language by one who is among the foremost investigators of the phenomena with which the book deals. The manner of origin of this book makes it natural that the author should illustrate the various principles of heredity by examples from his own extensive experiments, whenever such examples are available, and this method gives the book a unique value.

The brief introductory chapter on "Genetics a new science" recognizes the profound influence exercised by the theory of evolution in many fields of human activity, and shows how the evolutionary idea has forced man to consider his own probable future and to seek to control that future. As the "existence of civilized man rests ultimately on his ability to produce from the earth in sufficient abundance cultivated plants and domesticated animals," "civilization may be advanced in a very direct and practical way" by an increased knowledge of plant and animal breeding. To the solution of the problem "how to create new and improved breeds better adapted to the conditions of present-day agriculture," and especially to an exposition of the "operations" of Mendel's law of heredity, the author specifically addresses himself.

Chap. i on "the duality of inheritance" defines heredity as "organic resemblance based on descent," and discusses fertilization, pointing out that either eggs or sperms can under certain experimental conditions produce a complete organism without union with another gamete, and that such a result is realized regularly in nature in the case of male bees and wasps. The x and $2x$ generations of LOTSY are then considered under the designation N and $2N$ generations, a change of terminology which has nothing to commend it. Chap. ii distinguishes between "germ-plasm" and the body or "soma," and cites experiments in the transplantation of eggs to an alien soma as proof of

[1] CASTLE, W. E., Heredity in relation to evolution and animal breeding. 8vo, pp. xii+184. *figs. 53*. New York: D. Appleton & Co. 1911.

the correctness of WEISMANN's contention that "body and germ-cells are physiologically distinct," and that "body (or somatic) influences are not inherited." The next six chapters deal with "the greatest single discovery ever made in the field of heredity, Mendel's law," with illustrations drawn chiefly from the author's experiments with guinea-pigs, rabbits, rats, and mice. After a careful statement of the general principles with concrete examples, attention is given to the determination of dominance, heterozygous characters and their "fixation," atavism or reversion, evolution by loss or gain of characters, evolution of new races by variations in the potency of characters, modification of unit-characters by selection, and "blending" inheritance. This enumeration of the subjects treated suffices to indicate that the author's discussion is no merely formal presentation of the ramifications of the Mendelian system. Instead, it deals lucidly and entertainingly with a number of moot questions. It is pleasing to note that the author does not follow some other recent writers (BATESON, PUNNETT, DAVENPORT) in the view that dominance is always due to the presence of a gene which is absent from the recessive form. He mentions several cases for which this explanation is not available, and leaves the problem as to the cause of dominance unsolved. He is convinced that unit-characters may be modified by selection. He says (p. 120): "In several cases I have observed characters at first feebly manifested gradually improve under selection until they became established racial traits." While this must be accepted as an observed fact, the statement that it is due to selection is apt to be misleading. The difficulty remains that selection can only pick out individuals already possessing the observed degree of development of any characteristic under consideration, and does not in any manner modify the qualities which will be possessed by the offspring of the selected individuals. It only permits such individuals to reproduce to the exclusion of other individuals which do not have the character in question. Under "blending inheritance" the now well-known case of skull-size and ear-length in rabbits is discussed, and the view is expressed that in the light of experimental results of NILSSON-EHLE, EAST, and others, such cases of apparent blending may really prove to be segregating inheritance in which a considerable number of units are involved.

In chap. ix the effects of in-breeding are considered, and the reviewer's conception is indorsed, that the apparent deterioration is generally due to the formation of homozygous strains, whereby the stimulus is lost which comes from the "bringing together of differentiated gametes, which, reacting on each other, produce greater metabolic activity." In this connection the statement is made (p. 150) that "under self-pollination for one generation following a cross, half the offspring become homozygous; after two generations three-fourths of the offspring are homozygous"; and so on. This statement is misleading as it stands, and is literally true only in the case of monohybrids. A second cause recognized for deterioration following in-breeding is the appearance of recessive defects, such as albinism, etc., a cause which has been specifically pointed out by DAVENPORT.

The tenth and last chapter deals with heredity and sex. The hypothesis offered by the author several years ago that the female regularly possesses a chromatic element, or something else in addition to the possessions of the male, is made the key to the entire discussion of this subject, and a series of facts is presented which give the hypothesis considerable apparent plausibility, although the philosophical basis for it seems to the reviewer to be a little strained. This basis is found in the statement that the female as compared with the male has an additional function, namely the supplying of nourishment to the young zygote. On the other hand, it may be pointed out that the male differs from the female in many functions, and is in many respects morphologically and physiologically the superior sex, and it is possible to interpret these differences as additions to the female. If the egg has the added function of nourishing the young zygote, the sperm has the added function of motility, and there seems no better a priori ground for expecting an additional chromatin element to represent one of these additions than the other. The reviewer believes that there is no sufficient ground at present for the assumption that sex is always determined in the same manner. It cannot be determined as yet whether the basic differences between the sexes are quantitative or qualitative, and in either case the same results might be attained by any one of several different methods. The attempt to bring the sex-phenomena of all organisms under a single viewpoint is premature.

Each of the chapters is followed by a "bibliography," but the meagerness of the literature lists may be judged from the fact that they include only 46 titles from 26 authors, including 14 of CASTLE'S own papers. This may be compared with the bibliography appended to another recent book on heredity which includes 426 titles from 170 authors. However, this is not intended as an adverse criticism of CASTLE'S excellent book, but is mentioned to show the limitations of its author's aims. Extensive literature lists are indispensable to students, but would defeat their own purpose in a book intended primarily for popular reading.

The press work is excellent and typographical errors are few, though "reversion" is rendered "revision" in the heading of chap. iv.—GEORGE H. SHULL.

NOTES FOR STUDENTS

The mycoplasma theory.—In spite of many attempts to establish the truthfulness or fallacy of ERIKSSON'S mycoplasma theory, its status has not been definitely settled, and it continues to be a subject of controversy. An outline of the history and the present status of the theory is presented by ERIKSSON[2] in a brief article occasioned by MARESCHKOWSKI'S[3] appropriation

[2] ERIKSSON, J., Über die Mykoplasmatheorie, ihre Geschichte und ihren Tagesstand. Biol. Centralbl. **30**:618–623. 1910.

[3] MARESCHKOWSKI, C., Theorie der zwei Plasmaarten als Grundlage der Symbiogenesis. Biol. Centralbl. **30**:278 ff. 1910.

of the term *mycoplasma* to designate one of the two types of protoplasm which he conceives to be the fundaments of which the organic world is built up. The article is a convenient historical summary but adds no new material to what has already been published. In it the author again calls attention to the fact, often emphasized by him, that the study of secondary rust pustules, as carried out by WARD and others, cannot have any bearing on the theory which is concerned only with the origin of the primary pustules. In concluding the author expresses a wish for a complete investigation of the whole problem.

ZACH,[4] in a paper dealing with the results of a cytological investigation of the pustules of *Puccinia graminis* and *P. glumarum*, comes to the conclusion that the mycoplasma theory is untenable and rests on a misinterpretation of the facts which, in themselves, he concedes are correctly described by ERIKSSON. ZACH studied microtome sections and free-hand sections of *P. graminis*, but only free-hand sections of fixed material of *P. glumarum*. From this material he describes processes of disorganization of the tissues. At the margin of the rust pustules the host cells have a turbid, deeply staining protoplasm which he identifies with ERIKSSON's resting mycoplasma. The nuclei of these cells are much hypertrophied and seem to be filled with hyphae, some of which extend to the cell wall. The filaments degenerate and fuse into irregular lumps. The nucleus decreases in size and finally becomes an amorphous homogenous body termed an excretion product. Similar smaller bodies occurring throughout the cell he regards as identical with the "plasmanucleoli" of ERIKSSON. In more advanced stages the hyphae are largely dissolved, leaving only small amorphous particles. These processes, by which the cell and the parasite mutually destroy each other, resemble those formerly described by the author in his studies on the root tubercles of cycads. The process is termed phagocytosis, analogous to that phenomenon in animals. The figures accompanying the paper represent in a general way processes in cells undergoing disorganization as the result of the action of the fungi or other agents, which cause a slow dying of the cells. The "hyphae" figured bear not the least resemblance to the hyphae or haustoria of rusts.

In a criticism of the foregoing paper, ERIKSSON[5] points out that ZACH fails to state that he confined his studies to the primary uredo pustules, and furthermore that the pustules investigated by him were too far advanced to show stages of the mycoplasma, which is present only before the pustules become visible. The formations observed by ZACH belong to a later stage in the life of the rust. The various "excreted" bodies described by ZACH, ERIKSSON finds

---

[4] ZACH, F., Cytologische Untersuchungen an den Rostflecken des Getreides und die Mycoplasmatheorie. Sitzungsb. K. Akad. Wiss. Wien Math.-Naturw. Kl. **119**:307–330. *pls. 2.* 1910.

[5] ERIKSSON, JAKOB, F. ZACH's cytologische Untersuchungen über die Rostflecken des Getreides und die Mycoplasmatheorie. Sitzungsb. K. Akad. Wiss. Wien Math.-Naturw. Kl. **119**: pp. 8. 1910.

only in advanced stages of cell disorganization, and not during the mycoplasma stage. ERIKSSON also fails to find "hyphae" in the disorganizing nucleus, but believes the structures interpreted as such by ZACH to be chromatin threads.

A paper by BEAUVERIE[6] relates to the "plasmanucleoli" described by ERIKSSON. BEAUVERIE finds in the cells of fungi certain granules stainable with basic dyes, which he terms "corpuscules métachromatiques." In wheat plants attacked by rust he finds similar bodies in the mycelium, and in the host cells in the regions invaded by the fungus, but not in the normal cells. These granules he identifies with the plasmanucleoli of ERIKSSON. Just how giving these bodies a new name would, in itself, invalidate ERIKSSON'S interpretation or constitute a new interpretation is not easy to see.

The solution of the problem which gave rise to the mycoplasma theory probably lies in the direction suggested by the recent work of PRITCHARD[7] on rust-infected grain seeds. PRITCHARD finds that rust-infected wheat seeds, to which little attention has been given from this viewpoint, contain living mycelium in the neighborhood of the rust sori. When such seeds are planted the fungus resumes its activity with the growth of the seedling, and penetrates both the stem and root of the young plant. It also grows in the spaces between the leaf sheaths. The formation of new uredo pustules from this mycelium has not been observed, nor have rusted wheat plants been obtained from infected seed grain under conditions rigorously excluding external infection.—H. HASSELBRING.

Spermatogenesis in Bryophytes.—WILSON[8] has completed his studies of spermatogenesis in *Mnium hornum* and also has investigated spermatogenesis in *Atrichum undulatum* and *Pellia epiphylla*. Because of the somewhat remarkable statements of J. and W. Docters VAN LEEUWEN-REIJNVAAN that centrosomes are constantly present in the spermatogenous cells in several species of *Polytrichum* and *Mnium*, and that in the ultimate division of these cells a reduction takes place whereby the haploid number of chromosomes is reduced to half (in *Polytrichum* to 3, and in *Mnium* to 4), these later divisions were studied with exceeding care.

In *Mnium hornum*, in the early stage of the penultimate division in spermatogenesis, a body is cut off by constriction from the nucleolus. In earlier divisions of the spermatogenous cells this division of the nucleolus was not observed. This body was never discovered outside of the nucleus and soon

[6] BEAUVERIE, J., L'hypothèse du mycoplasma et les corpuscules métachromatiques. Compt. Rend. **152**:612–615. 1911.

[7] PRITCHARD, F. J., The wintering of *Puccinia graminis Tritici* E. & H. and the infection of wheat through the seed. Phytopathology **1**:150–154. *pl. 1. fig. 1.* 1911. See also BOT. GAZ. **52**:169–192. *pl. 1.* 1911.

[8] WILSON, MALCOLM, Spermatogenesis in the Bryophyta. Ann. Botany **25**:415–457. *pls. 37–38. figs. 3.* 1911.

disappears. During prophase of the ultimate division of the spermatogenous cells, the nucleolus divides into two separate masses by constriction, and before separation is complete, a third small body buds off from one of the nucleolar bodies. These three bodies become free, but do not pass beyond the nuclear membrane, and the smallest one is considerably larger than is usually associated with centrosomes. These bodies were lost during later prophase, and their fate could not be determined. Chromosomes are constantly 6 in number and no difference in size could be observed.

The daughter nuclei at first contain several deeply staining granules, which later are replaced by a single centrally placed nucleolus. This nucleolus divides by constriction into two bodies, one of which again divides. The nuclear membrane then becomes indistinct, and two of the nucleolar bodies pass out into the cytoplasm, and probably increase by division, as more than two can often be found. Later they become rodlike and are usually grouped near a vacuole. At this stage the nucleus is barely distinguishable as a mass somewhat denser than the surrounding cytoplasm. The nucleolus may again cut off one or two bodies, which probably pass out into the cytoplasm and become associated with the rodlike bodies. These rods now increase in length, become irregularly curved, and look very much like chromosomes. Their number is usually three or four. This situation would seemingly explain the double reduction of J. and W. Docters VAN LEEUWEN-REIJNVAAN. The nucleolus now enters upon a third period of division, giving rise to two bodies which pass out into the cytoplasm, one being most likely the blepharoplast; the other WILSON thinks is perhaps the same as the "Nebenkörper" described in *Marchantia* by IKENO. All but one or two of the rodlike bodies now coalesce and form a spherical mass, which the author names the "limosphere." Later, when the limosphere is seen in optical section, it appears as a ring. In the last stages studied (the nearly mature sperms) the limosphere still persisted.

In *Atrichum undulatum* the sequence is much the same as in *Mnium*. No centrosomes could be found, and the chromosome number is 17. In *Pellia epiphylla*, centrospheres and perhaps centrosomes are present in later divisions in the antheridium. The author thinks the blepharoplast may be derived from the centrosome. A limosphere and accessory body are present in the sperm, but their origin was not determined.

WILSON's work gives evidence of extremely careful study, and seems to furnish a satisfactory explanation for the fantastic performances which have been reported as taking place during spermatogenesis in Musci.—W. J. G. LAND.

Origin of the mitotic figure.—LAWSON's[9] study of the microspore mother cells of *Disporum*, *Gladiolus*, *Yucca*, *Hedera*, and the vegetative cells in the root tip of *Allium* has revealed a series of stages in the development of

[9] LAWSON, A. ANSTRUTHER, Nuclear osmosis as a factor in mitosis. Trans. Roy. Soc. Edinburgh **48**:137–161. *pls. 1–4*. 1911.

the mitotic spindle which have never before been described. These new stages are to be found in the prophase immediately preceding the organization of the equatorial plate, and concern the fate of the nuclear membrane. Many authors have either described or figured the breaking down of the nuclear membrane at a time when the multipolar stage has been reached, or in vegetative cells when the polar caps have been completely formed. Contrary to the generally accepted view, LAWSON finds that the nuclear membrane does not break down or collapse at any period during the spindle development, but behaves as one would expect a permeable plasma membrane to behave under varying osmotic relations.

The nucleus is regarded as an osmotic system, and its membrane constitutes an essential element in that system. As the prophase proceeds, the nucleus or the nuclear vacuole, as he calls it, becomes smaller and smaller, and the membrane gradually closes in about the chromosomes, which later become crowded together around the nucleolus. When the karyolymph becomes so much reduced that it is no longer visible as a clear nuclear sap, the membrane becomes closely applied to and completely envelops the surface of each chromosome. As a consequence, instead of a single osmotic system represented in the nucleus, there have been established now as many independent osmotic systems as there are chromosomes.

The gradual diminution of the nuclear vacuole brings about a condition where a limited amount of cytoplasm of reticulate structure is obliged to occupy a space which has greatly increased by the reduction in volume of the nuclear vacuole. This necessarily sets up in the cell a tension sufficient to cause a readjustment and a changed configuration in the reticulate form of the cytoplasm, and therefore the cytoplasm in the region of the nuclear wall, drawn out from the reticulum by the receding membrane, becomes changed to the form of fine threads or fibrils of the "kinoplasm." The lines of tension are constantly shifting throughout the prophase. Such a shifting does not mean the changing of the threads bodily from one position to another, but it means the relaxing of the tension along certain threads, which would consequently fall back into the reticulate forms, and the setting up of new lines of tension by the drawing out of threads from the hitherto undifferentiated reticulum. Thus not only individual threads, but entire cones of fibrils may appear to assume different positions. The attachment of the spindle fibrils to chromosomes is brought about by the enveloping of each chromosome by the receding membrane.

Taking all the stages observed into consideration, the author concludes that the achromatic spindle in vascular plants is simply an expression of a state of tension in the cytoplasm, and that this tension is caused in the first place by nuclear osmotic changes that create a condition where a limited amount of cytoplasm is obliged to occupy an increased space. Thus, he regards the achromatic figure as not an active factor in mitosis, but nothing more than a passive effect of nuclear osmotic changes.—S. YAMANOUCHI.

The fossil conifers of Spitzbergen.—An important contribution by GOTHAN[10] contains a description of the fossil woods of various geological horizons from the island of Spitzbergen, brought back for the most part by Arctic expeditions during the past 50 years. The most interesting woods from the evolutionary standpoint are those from the Upper Jurassic of Green Harbour, Esmarks Glacier, and Wimansberg. Of these the author remarks: "Es ist überhaupt gemein auffallend, wie häufig man in der Hoftüpflung zahlreicher Hölzer der oberen Juraformation des Nordens Araucarioiden Charackteren begegnet, und dies bei Angehörigen von Familien, die mit den Araucarieen im übrigen sicher weiter nichts zu thun haben" (p. 18). The author holds that strongly pitted rays, together with normal or traumatic resin canals in the wood, are an infallible indication of abietineous affinities. Since most of the woods which he describes in this memoir have these characteristics, he puts them with the Abietineae, in spite of the fact that other apparently more important features are clearly araucarian. It is interesting to note in this connection that SEWARD[11] has referred woods of a similar type from the Upper Jurassic of Yorkshire in England to araucarian affinities. There seems little reason to doubt that SEWARD rather than GOTHAN is right in this matter, especially as it appears from recent studies on the living Araucariineae, as yet unpublished, that these came from ancestors which, on comparatively anatomical evidence and in accordance with generally accepted morphological principles, possessed bars of Sanio in their tracheids, wood parenchyma, opposite pitting, resin canals in the wood, strongly pitted rays, and a clearly double system of ovulate cone scale bundles, all characters unmistakably abietineous. It is accordingly not surprising to find intermingled araucarian and abietineous characters in the araucarian woods of the Jurassic. Moreover, if one admits that GOTHAN'S jurassic woods are in reality abietineous and not araucarian, a grave difficulty arises in the case of recently described woods from the American Cretaceous, such as *Brachyoxylon*, *Araucariopitys*, *Paracedroxylon*, etc., which sometimes have ligneous resin canals and sometimes lack them, and likewise have both the araucarian and the abietineous types of ray, the former being more abundant in these later woods. The facts can all be squared with a derivation of the Araucariineae from the Abietineae, but not with the reversed derivation. The most interesting of the new genera and species described in this memoir are *Protopiceoxylon* (*P. extinctum*, apparently beyond question araucarian), *Protocedroxylon* (*P. araucarioides*), and *Cedroxylon* (sic!) *transiens*. It seems quite clear from this and other publications of GOTHAN on the Jurassic woods of northern Europe that the Araucariineae were at that period not very remote from their abietineous source. It follows

[10] GOTHAN W., Die fossilen Holzreste von Spitzbergen. Kung. Svensk. Vetensk. Handl. **45**: no. 8. 1910.

[11] British Museum catalogue of Mesozoic plants, Jurassic flora. II. Liassic and Oolitic floras of England. *pls. 6, 7*. London. 1904.

that the so-called Araucarioxyla of the earlier Mesozoic have nothing to do with the evolution of the stock from which *Agathis* and *Araucaria* have been derived. *Walchia* and *Voltzia* from the Permian and Trias, moreover, do not present the *Araucarioxylon* type of wood. The situation thus becomes difficult indeed for those who believe the Araucariineae to be the oldest conifers, and to constitute the articulation of the family with the Cordaitales.—E. C. JEFFREY.

Cytology of the Chytridineae.—BALLY,[12] working in STRASBURGER'S laboratory, has added much of importance to our knowledge of the cytology of the Archimycetes. In *Synchytrium taraxaci* the primary nucleus divides, not by mitosis as in *S. decipiens* and *S. puerariae*, which have been investigated by STEVENS and KUSANO, but by a process analogous to nuclear gemmation, in which masses of chromatin originally derived from the nucleolus pass into the cytoplasm as chromidia which later become the basis of the secondary nuclei. While the stages in this process are not fully worked out, there can be little doubt from the figures showing the old primary nucleus still undivided, together with scores of secondary nuclei in the same parasite, but that the description given is substantially correct. These nuclei later divide by mitosis and always have four chromosomes. Curiously enough the conspicuous asters ("karyodermatoplasts") which reconstruct the nuclear membrane in *S. decipiens* and *S. puerariae* appear to be absent from *S. taraxaci*.

BALLY does not follow PERCIVAL[13] in including *Chrysophlyctis* in *Synchytrium*, but he fully confirms and substantiates PERCIVAL'S account of the remarkable amitoses in the resting sporangia of that plant. Here nuclear gemmation reaches its climax. The extruded chromidia never organize secondary muclei, but pass unchanged into the zoospores, which are formed in a most peculiar manner, while the remains of the primary nucleus still persist undivided in the center. Here again more details would be very welcome, but it is clear from the figures, together with those of PERCIVAL, that there is something here far different from the ordinary behavior of nuclei, or better of chromatin, for such cysts may be said to have no nuclei, though rich in chromatin.

In *Urophlyctis Rübsaamenii*, amitosis, largely by nuclear gemmation of which figures showing details are presented, appears to be the sole method of nuclear multiplication. The cytological condition of this plant contrasts sharply with that of the two preceding, in that the parasite becomes coenocytic with the beginning of growth. On the basis of such differences he separates the Archimycetes into two series: one essentially uninucleate, including *Synchytrium* and *Chrysophlyctis;* the other coenocytic from almost the beginning, including the Cladochytriaceae, and more doubtfully the Rhizidiaceae

[12] BALLY, WALTER, Cytologische Studien an Chytridineen. Jahrb. Wiss. Bot. **50**:95–156. *pls. 1–5. figs. 6.* 1911.

[13] PERCIVAL, JOHN, Potato wart disease: the life history and cytology of *Synchytrium endobioticum* (Schilb.) Percl. Centralbl. Bakt. **25**:440–446. *pls. 1–3.* 1910.

and Olpidiaceae, with perhaps also the Hyphochytriaceae. He follows PAVILLARD in believing that the Synchytriaceae show most similarity in cytology to the Sporozoa, and were probably derived from them, but he does not commit himself to any opinion concerning the origin of the second group. —ROBERT F. GRIGGS.

Movement of water.—The ascent of water in vessels containing chains of water and air bubbles (Jamin's chain) may take place in one of two ways: either the whole chain moves upward or the water alone moves while the air bubbles are stationary. SCHAPOSCHUIKOFF[14] claims that the physical conditions of a Jamin's chain in the conducting vessels of plants are not such that they prevent the movement of the chain as a whole. Reasoning theoretically, he concludes that the presence of cross walls in the vessels do not hinder such a movement. The bubble just above the cross wall and the one just below are under unequal pressures, the former under reduced pressure owing to the suction from above, and the latter under increased pressure owing to the rise of water below. On account of the increased pressure the bubble below goes into solution, passes through the cross wall, and separates out again under the reduced pressure above. It is assumed that the bubbles arise only from gases dissolved in the water filling the vessel. They separate out when the water consumption by the plant is greater than the supply, causing a reduced pressure in the vessels.

The author constructed a very ingenious apparatus to put the above theoretical conclusions to the test of experimental proof. In his apparatus gas bubbles began to form from the gases in solution when the pressure reached one-half to one-third of an atmosphere in a glass tube corresponding to a conducting vessel in the plant. As soon as a gas bubble reached the cross wall, the filtration of water through the membrane ceased. The manometer soon showed an increased pressure in the tube, due to the continued rise of water from below. After a short time the bubble went into solution and passed through the water-saturated membrane, allowing the filtration of water to continue. The manometer now showed a sinking of pressure again. The passage of the bubbles by the sculpturing of the wall may be explained in a way similar to their passage through the cross walls. As soon as a bubble is held by a thickening in the wall, unequal pressures are set up, causing it to dissolve sufficiently to pass on.—CHAS. O. APPLEMAN.

Chaparral.—A woodland consisting of stunted trees, seldom more than 10 feet, and apparently a response to the peculiar conditions of Southern California, has been studied by PLUMMER,[15] and a report made upon its impor-

---

[14] SCHAPOSCHUIKOFF, WALK., Sollen die Luftblässchen der sogenannten Jaminschen Kette in den Leitungsbahnen der Pflanzen für immobil gehalten werden? Beih. Bot. Centralbl. **27**:438–444. *figs 2.* 1911.

[15] PLUMMER, FRED G., Chaparral. U.S. Dept. Agric., Forest Service, Bull. 85 pp. 48. 1911.

tance in conserving moisture and regulating the flow of streams in a region where the water supply is of the utmost economic importance. This conservation is accomplished by the root system penetrating the soil and assisting percolation, while at the same time the trees prevent erosion by shading the ground, by breaking the force of hot winds, and by lessening evaporation. The most active destructive agent is fire, which rapidly sweeps the half-dry vegetation from the arid mountain slopes. The investigator offers good arguments in support of his belief that the protection of the chaparral cover is of great importance in preventing the loss of water needed for irrigation.

From the ecological viewpoint, the "true chaparral," which seems to be a climatic formation holding complete possession of its domain and found principally in California, is distinguished from "mock chaparral," which is a pioneer association of similar dwarfed trees occurring in the forest succession in parts of Arizona, New Mexico, Colorado, and Utah. In both the same genera and often the same species of sclerophyllous trees are to be found. The dominant members are various species of *Adenostoma*, *Arctostaphylos*, *Ceanothus*, and *Quercus*, while forms of *Rhus*, *Cercocarpus*, *Rhamnus*, and *Ribes* are among those of secondary importance.

The study includes a consideration of the ecological relations and relative economic importance of the more abundant species, of the methods of controlling fires, of restocking after fires, and of the possibility of introducing larger tree species. A map shows the distribution of this interesting forest formation in California.—GEO. D. FULLER.

Stems of Diplolabis and Metaclepsydropsis—GORDON[16] has described the hitherto unknown stems of *Diplolabis Römeri* and *Metaclepsydropsis duplex*, as well as the attachment and vascular supply of their leaves. The stem in both species is a long dichotomous rhizome, with nodes only at wide intervals. The stele, circular in section, is in *Diplolabis* composed entirely of tracheids, while in *Metaclepsydropsis* there is much parenchyma scattered among the small central xylem elements. The leaf trace departs in each case as an elliptical strand with two lateral mesarch protoxylems. In the lower portion of its course, it may resemble in turn the petiolar bundles of *Clepsydropsis*, *Dineuron*, or *Zygopteris;* but after its entrance into the petiole it assumes, respectively, the typical "H" of *Diplolabis* and the "dumb-bell" of *Metaclepsydropsis*. The changes in structure presented by the foliar bundle as it ascends from node to petiole, and the striking similarity at the base of the leaf trace between these two species, and indeed among all the Zygopterideae, furnish further evidence of the conservatism of this region and of its importance as a seat of ancestral characters.—E. W. SINNOTT.

[16] GORDON, W. T., On structure and affinities of *Diplolabis Römeri* (Solms). Trans. Roy. Soc. Edinburgh 47^4:711–736. *pls. 1–4.* 1911.

———, On the structure and affinities of *Metaclepsydropsis duplex* (Williamson). Trans. Roy. Soc. Edinburgh 48^1:163–190. *pls. 1–4.* 1912.

Anatomy of Osmundites.—SCHUSTER[17] has described the anatomical structure of a new species of *Osmundites* (*O. Carneri*) from Paraguay. He considers it an "ectophloic siphonostele," and calls especial attention to the absence of leaf gaps. A ring of xylem, unbroken but very thin opposite the wide "rays," is figured in a text diagram, but it is noteworthy that the attachment of leaf trace to stele has not been drawn. The plates of photographs, however, show broad and indisputable leaf gaps formed by the departure of leaf traces which are thin and arched from the very first. The preservation of tissues other than the xylem is not good enough to determine the presence or absence of internal phloem, but the wide gaps and other striking resemblances between the stele of this species and that of *Osmundites skidegatensis*, where internal as well as external phloem is well developed, would lead one to suspect very strongly the existence of this tissue in *O. Carneri*. There is doubt as to the horizon of the new species, but its author places it as probably Tertiary, though possibly Jurassic. Species of *Osmundites* have now been described from the continent of Europe, western Canada, Paraguay, South Africa, and New Zealand.—E. W. SINNOTT.

Respiration and wounding.—SCHNEIDER-ORELLI[18] finds that wounding apples, pears, and potatoes which are no longer capable of forming wound periderm increases the amount of carbon dioxide given off by such fruits and tubers above that normally given off. He concludes, therefore, that the increased respiration is due to wounding alone, and not to renewed cell division which follows wounding in tissues which are still capable of growth. An attempt to apply the same idea to the study of the stimulation of respiration due to infection by fungi gave no results, since it was impossible to separate the carbon dioxide produced by the fungus from that produced by the host.—H. HASSELBRING.

A glucoside.—Saponarin, a glucoside of the formula $C_{21}H_{24}O_{12}$, has been found in 24 species of phanerogams (8 families) out of more than 1300 species examined. It is contained in the epidermis of leaves and stains blue to violet with IKI. MOLISCH[19] now finds it in *Madotheca platyphylla*, the only liverwort out of 36 species examined. Its peculiar distribution in the plant kingdom and its liability of being mistaken for soluble starch make it of interest. It should be stated that the writer's microchemical methods do not prove that this substance is saponarin.—WILLIAM CROCKER.

---

[17] SCHUSTER, J., *Osmundites* von Sierra Villa Rica in Paraguay. Ber. Deutsch. Bot. Gesells. **29**:534–540. *pls. 2.* 1911.

[18] SCHNEIDER-ORELLI, O., Versuche über Wundreiz und Wundverschluss an Pflanzenorganen. Centralbl. Bakt. II. **30**:420–429. 1911.

[19] MOLISCH, HANS, Über das Vorkommen von Saponarin bei einen Lebermoos (*Madotheca platyphylla*). Ber. Deutsch. Bot. Gesells. **29**:487–491. 1911.

VOLUME LIII NUMBER 6

THE

BOTANICAL GAZETTE

JUNE 1912

THE FORMATION OF MECHANICAL TISSUE IN THE TENDRILS OF PASSIFLORA CAERULEA AS INFLUENCED BY TENSION AND CONTACT

W. D. BRUSH

(WITH THREE FIGURES)

Introduction

The mechanical theory of growth, as put forth by SACHS (20), has of late years been replaced by the idea of self-regulation in the plant depending upon external stimulus. This idea is followed quite closely by PFEFFER (18).[1] As a consequence, considerable attention has been directed to the effect of strain upon plant tissues, since by this new theory we might expect the plant to respond to a state of strain by a greater development of strengthening tissues. The present investigation was undertaken to determine if such self-regulation is present in the tendril that stronger mechanical tissues are produced where needed. To state the problem of the present paper: Do tendrils which are functioning to support the plant possess greater strength than those which have grasped no support, and if so, how is this strength increased, and is it due to tension or to contact, or to a combination of both?

DARWIN (5) observed that tendrils which have grasped no support soon die; WORGITZKY (26, p. 39) noted a greater breaking strength of tendrils with a support over those without. Otherwise, no attempt has been made to answer this question.

[1] For a discussion of these two theories see NEWCOMBE (15).

Historical

The first observations to determine the effect of strain upon the plant were by KNIGHT (12) in 1803, when he allowed fruit trees to sway in the wind in one plane only and obtained a greater increase in wood on the two sides in the direction of swaying; this he considered to be due to a greater movement of sap through a loosening of the cells, a merely mechanical process.

In 1879 BARANETSKY (2), investigating the periodicity of growth, found that when a small amount of tension (10–30 grams) was applied to a stem, it had the effect of retarding the growth in length.

SCHOLTZ (21) confirmed these observations, but found that two results were produced: first an acceleration and later a retardation of growth; the first result he attributes to a rapid growth of the cell-membrane, the second to a pathological condition in which the building up of the materials is hindered.

HEGLER (8), working along the same lines, found that this retardation of growth bears a close relation to the daily periodicity in elongation of the stem. This, he says, demonstrates that tension calls forth a response in the cell, hence is a true irritation stimulus.

HEGLER (9) also investigated the effect of tension upon the anatomical structure of stems. By gradually increasing tension on seedlings of various plants, he found that the breaking strength was in many cases nearly doubled in three days, due to an increase in amount of the collenchyma, sclerenchyma, and bast, a much greater increase than takes place under normal conditions.

BALL (1) later repeated HEGLER'S work and found no increase in mechanical tissues even in the plants with which HEGLER worked.

HIBBARD (10), also working along the same lines, found no increase in mechanical tissues with tension except in one plant (*Vinca*), where a slight increase was noted.

The work of VÖCHTING (23) upon *Helianthus annuus*, of WIEDERSHEIM (25) upon woody stems, and of KELLER (11) upon fruit stalks has likewise shown no response due to tension.

Later work by BORDNER (3) seems to show an actual increase in breaking strength and in amount of mechanical tissue in the several species with which he worked. This investigator, by the

use of a large number of individuals in each experiment, has, we believe, demonstrated that there is an actual response of the plant to tension, by which stronger tissues are laid down and the tensile strength of the part under tension increased, though not to such an extent as HEGLER's results seem to show.

Another line of investigation on the effect of tension has been followed in a comparison of the cells on opposite sides of a stem which has been prevented, by weighting, from responding to a heliotropic or negative geotropic stimulus (BALL **1**, pp. 326 f.). In this case a thickening of cell walls occurs on the convex or upper side of the stem, which has been believed by some to be due to a state of tension. A similar thickening occurs (BALL **1**, p. 339) on the upper side of a stem in a plaster cast placed horizontally, also in the concave portion of a stem which has formed a curve. In the last case cited, BALL demonstrated that no increase in breaking strength of the stem took place, a fact which he attributes to the concave side being built up at the expense of the convex side. This is substantiated by the investigations of PENNINGTON (**16**) on the effect of compression on plant stems, where he finds a reduction in the thickness of cell walls due to compression.

While a number of investigators have thus studied the effect of mechanical strain upon tissues in stems, the investigations on tendrils have been almost exclusively for the explanation of external movements, such as the cause of coiling, etc. (For explanation of external phenomena see FITTING **7**, DEVRIES **6**, and MACDOUGAL **13**.) The anatomical structure has been worked out in a comparative manner by MÜLLER (**14**) and WORGITZKY (**26**), but only by the latter writer was the tendril treated in relation to its function.

DARWIN (**5**, p. 58) noted that in petiole climbers the petioles are thickened from contact, and TREUB (**22**, p. 65) found marked changes in the anatomical structure of the portion of the petiole in contact, consisting in a greater development of the mechanical system, which is borne out in a general way by the later work of VON DERSCHAU (**24**).

MÜLLER (**14**), in his study of the tendrils of the Cucurbitaceae, found that contact produced earlier and greater lignification of sclerenchyma in the free portion on the under side (p. 127).

WORGITZKY (**26**) is the only investigator who tested the breaking strength of tendrils with and without a support. He noted that a *Passiflora* tendril which had grasped a support broke at 600 grams, while one free from a support broke at 350 grams. A tendril of *Cucurbita Pepo* likewise seemed to show greater strength of tissues when a support had been grasped. Even supposing that these tendrils tested were of the same age (which is not stated by the author), these data have little value in the present paper, since it is not known whether the tendrils with a support were under tension or contact alone. WORGITZKY found in his anatomical study that marked anatomical differences come in with the grasping of a support. As to the cause of these anatomical differences, none of these investigators have written. VON DERSCHAU (**24**) by an ingenious method sought to separate the influence of tension from that of contact in his experiments with petiole twiners, by attaching a clamp to the leaf and suspending a weight thereon. Contact alone was secured by allowing a petiole merely to twine around a stick. It was found that contact alone or tension alone, gradually increased, called forth a greater development of mechanical tissue, a still greater increase taking place with the combination of both factors. It seems doubtful, however, whether the contact stimulus was avoided by this method of experimentation.

Methods

Experiments were conducted in the greenhouse under very constant and favorable conditions for growth.

Special care was taken to secure proper controls, since among tendrils, as throughout the plant kingdom, much variation occurs in size and vigor of individuals; however, it was found upon investigation that tendrils on the same vigorous vine within two or three internodes do not vary to an appreciable amount; this conclusion was based upon a comparison, by means of camera drawings, of sections of the ring of mechanical tissue of several tendrils on the same vine and on different vines, all under the same conditions (a weight of 15 grams) and all of the same size and vigor. These drawings show the areas of mechanical tissue of tendrils near each other on the same vine to coincide practically,

while those from different vines have different areas. The reliability of this method of securing controls is also shown by a comparison of the breaking strength of tendrils from the same and from different vines, which shows tendrils on the same vine under the same conditions to correspond quite closely in tensile strength.

Measurements were also taken to secure proper controls, but it was found that healthy tendrils on the same vine varied only slightly in rate of growth, and were ready for contact at approximately the same age. As the time when the tendril is most suitable for contact can be judged within 24 hours, and since the time between the maturing of tendrils on successive nodes is quite constant, a very uniform method of starting the experiment on each tendril was obtained. Moreover, when tension was applied, a certain scheme for weighting was used, to secure gradually increased tension at the same rate in each case. The experiment on each tendril was closed at exactly the same length of time from the date when it was begun, and note of weather conditions was taken during the time of experiment.

Tendrils which had been under experiment were compared by two methods: (1) by their breaking strength, and (2) by their anatomical structure. The breaking strength was obtained by wrapping the extremities of the portion to be tested with damp cotton dipped in plaster of Paris; each end was then fastened between a pair of wooden blocks, made for the purpose, which were screwed tightly together; this preparation was then placed on a machine for breaking; one of the blocks was connected to a rod on which a thumbscrew was turned, to secure gradually increasing tension; the other block was connected to a spring balance from which was read the degree of tension at which the tendril broke. A straight portion of the tendril was always taken for testing. When the break occurred at the place of attachment of the tendril, the result was thrown out.

Cross-sections of tendrils were made and microphotographs taken at a magnification of 100 diameters. This shows well the form and arrangement of the mechanical tissues. Camera sketches of the area of mechanical tissue were also made and compared with microphotographs of the same tendrils in the study of the cross-

sections. Thickness of walls was also measured with the camera lucida, and special note was taken in the anatomical study of the number and size of cells in the ring of mechanical tissue.

Tendrils were placed under tension of different degrees by causing a tendril to coil about a short piece of reed supported at either end by a wire, to which was attached a cord and the same run over a pulley, the weight desired being attached to the other end of the cord. Contact without tension was obtained by the use of a counter-balance. Unless otherwise stated, tension and contact were always secured by this means.

When a ligature was used to secure tension, a strip of soft cotton flannel was wrapped about the tendril, and the string secured by a series of hitches only tight enough to grip the tendril firmly. This was found not to injure the tendril in the least, since it develops a soft cushion of tissue at the place of contact; moreover, in *Passiflora* a greater number of xylem cells is always produced at the place of contact, which tends to prevent any injury to the tissues. Sections taken at the place of ligaturing, except where too heavy weighting was introduced, showed the mechanical tissues to be normal, and the outside diameter often greater at this place than either immediately above or below.

A series of experiments was set up to determine the effect of ligaturing on the development of mechanical tissues. Two sets of *Passiflora* tendrils were used for comparison; in the one set attachment was secured by allowing the tendril to coil about a support as already described, in the other a ligature was tied about the contact portion of the tendril, and the same amount of tension was applied to each. Breaking strengths of these tendrils are given in table I.

These results show a slightly greater average breaking strength in the ligatured tendrils over those coiled about a support; this increase is evidently due to individual variation. These experi- ...ts and observations on ligaturing show clearly that the tendril ...rs no injury whatever from this treatment. When ligatures ... used to eliminate the contact stimulus, they were applied in ... experiments one day, in others two days after the time when tendrils were most sensitive to contact. Carnoy's fluid (4)

was used for killing and fixing material, as this preparation penetrates woody tissues very rapidly. Sections were stained in

TABLE I

DURATION OF EXPERIMENT 32 DAYS; FINAL WEIGHT USED 20 GRAMS

	With support	With ligature
1	1050 grams	1200 grams
2	1050	975 1265
3	1275	1475
4	1350	1250
5	1425	1475
6	750	775 925
7	820	925
Average	1103 grams	1140.5 grams

anilin safranin in order to bring out clearly the lignified tissues. Permanent slides were made by mounting in Canada balsam.

Further detailed methods are given in each experiment.

Experimental work

DETAILS OF EXPERIMENTS

1. *Tendril free, with contact, with contact and tension.*—In the first series of experiments, tendrils were placed under the following three conditions: (1) without any contact whatever, (2) with contact alone, and (3) with contact and tension. In the last case, contact was secured by allowing the tendril to twine about a support as before described. The three tendrils of each set to be compared were chosen from the same vine according to the methods previously given. A final weight of 20 grams was chosen after a few preliminary trials, which showed that 20 grams was the highest weight which could be used on the average *Passiflora* tendril without producing a weakening effect. The breaking strength of these tendrils is given in table II.

These results show clearly an increase in breaking strength due to contact, and a still greater increase when tension is applied. We have yet to determine, however, whether this increase with tension is due to the longitudinal pull or to increased contact,

that is, to the increased radial pressure of the contact portion against the support, due to the pull of the weight.

TABLE II

DURATION OF EXPERIMENT 32 DAYS*

Free	Contact	Contact and tension (20 grams)
I_1—112 grams	I_2— 775 grams	I_3—1425 grams
G_1—150	G_2— 725	G_3—1170
E_1—125	E_2— 850	E_4—1050
	E_3— 675	
F_1—450	F_3—1040	F_4—1275
H_1—740	H_2—1270	H_3—1350
D_1—390	D_2— 850	D_3—1095
	B_1— 900	B_2—1050
	A_2— 575	A_3—1200
K_1—120	K_2— 375	K_3— 400
M_1—152	M_3— 575	
N_1—240	N_2— 650	N_3—1275
L_1—100	L_2— 850	
	L_6— 660	
J_1— 75		
J_5—155	J_2— 450	J_3— 700
U_1—130	U_4— 970	U_3—1125
	V_1— 450	V_5—1110
W_1—185	W_2— 365	
X_1— 40	X_2— 575	
C_1—190		
C_2—110	C_4— 408	C_5— 905
C_3—145		
P_2—100	P_1— 760	
	R_2— 580	R_1— 705
O_1— 85	O_2— 420	
	O_7— 390	O_8— 660
	Q_1— 305	Q_8— 630
	Q_7— 490	
Average (20 tendrils), 190	Average (26 tendrils), 651	Average (17 tendrils), 1007

* Capital letters denote vines, subscripts denote tendrils, which were numbered consecutively on the vine from below upward.

2. *Middle third.*—To determine the influence of tension alone the following method was devised. In the one set a ligature was tied at the distance of a third the length of the whole tendril from the tip, and another the same distance from the base (fig. 1). To the distal ligature tension was applied by running the cord over a pulley, and from the proximal ligature a cord ran to the stem, which was made taut, so as to relieve the basal third of the

tendril from any strain. In the other set, the distal ligature was placed the same as the corresponding one in the first set, and a second ligature placed just below this. To the distal one tension was applied, and from the proximal one a cord ran to the stem, relieving the basal two-thirds of tension. By this device we have one tendril with the middle third under tension, the other with this portion not under tension, and the factor of contact the same in both, except that the proximal ligature is in a more sensitive part of the tendril in the second preparation than in the first, which would tend toward a greater development of mechanical tissue in the second preparation.

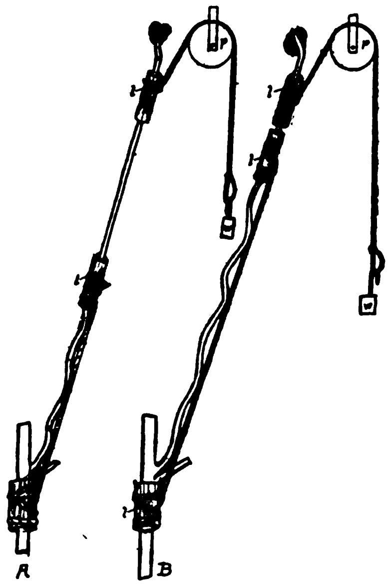


FIG. 1.—*A*, tension-tendril; *B*, tension-free tendril; *p*, pulleys; *l*, ligatures; *w*, weights.

Breaking strengths of the middle third of these tendrils are given in table III.

TABLE III

PERIOD 28 DAYS; FINAL WEIGHT 20 GRAMS

Under tension	Tension-free	Under tension	Tension-free
A_4—1100 grams	A_3— 875 grams	F_4—1275 grams	F_3— 950 grams
A_6— 950	A_5— 675	F_5—1090*	F_6— 900
A_8—1000	A_7— 700†	F_7—1200	F_8— 825
B_3—1475	B_2— 875	G_1—1625	G_2—1020
[B_4— 900]*	B_5— 900	G_3—1775	G_4—1000
B_7—1090	B_6— 650	G_5—1175*	G_6—1000
B_8— 900	B_9— 890	[G_7—1300]‡	
C_2—1075	C_3— 650	G_8—1535	
C_4—1075	C_5— 575	G_9—1425	G_{10}—1315†
C_7— 975	C_6— 725	G_{11}—1650	
D_4—1200	D_3— 625	H_2—1075	H_1— 735
D_5—1875	D_6— 850	H_3—1370	H_4— 865
D_8—1085	D_7— 710	H_5—1300	H_6—1685†
F_1—1325	F_2—1100		
		Average 1239	Average 862

* Broke at ligature. † Had to be broken close to base. ‡ Tension—coiled about a support.

With but one exception (H_6), these results show uniformly a decided increase in breaking strength of those under tension. The exceptional breaking strength of this tendril is partly accounted for by the fact that the break occurred in the basal third, which has a greater development of mechanical tissues. We can only conclude from these results that tension does produce greater strength of tissues in the middle third of the tendril.

3. *Basal third.*—The next experiments were for the purpose of determining the effect of tension on the less sensitive basal or proximal third of the tendril by the same method, only one ligature being used on the one under tension, however (fig. 2), and a counter-weight (*cw*) used in the one tension-free, instead of the cord being tied back to the stem. Breaking strengths of the basal third in the two sets of the tendrils are given in table IV.

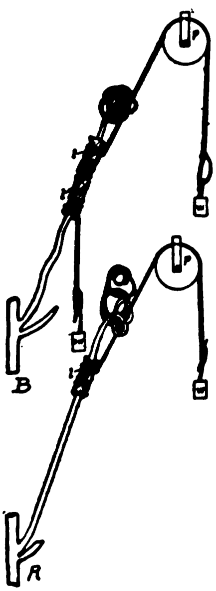


FIG. 2.—*A*, tension-tendril; *B*, tension-free tendril; *p*, pulleys; *l*, ligatures; *w*, weights; *cw*, counter-weight.

These results show no decided difference in strength between the two sets of tendrils compared as in the preceding experiments on the middle third. However, it is quite possible that the increase in strength of the "tension-free" tendrils in this experiment compared to the last is due to the tension stimulus received by the portion between the two ligatures, this stimulus being conducted through the tissues to the basal part; the contact stimulus is also greater here, due to the *two* ligatures compared to *one* in the tension tendril.[2]

In order to eliminate these additional stimuli the following method of experimentation was devised. Two loops of cord were made about the tendril not under tension at the same distance from the base as was the

[2] A study of sections of these tendrils (see below, under anatomical study) shows that these stimuli causing the formation of more mechanical tissue are actually transferred in the manner here stated.

TABLE IV

Series I

PERIOD 66 DAYS; FINAL WEIGHT 200 GRAMS

Under tension	Tension-free
A_4—1925 grams	A_5—1125 grams
A_8— 925	A_9—1450
B_3—1675	B_4—2150
B_7—1475	B_8—1775
G_4—2125	G_5—2000
G_8—1375	G_9—1550
Average 1583	Average 1675

Series II

PERIOD 32 DAYS; FINAL WEIGHT 50 GRAMS

Under tension	Tension-free
A_6—1890	A_7—1800
B_5—1490	B_6—1775
C_4—1260	C_5—1360
D_4—1150	D_5—1500
G_6—1600	G_7—1710
I_4—1930	I_5—1690
J_3—1270	J_4—1175
Average 1513	Average 1573

Series III

PERIOD 32 DAYS; FINAL WEIGHT 20 GRAMS

Under tension	Tension-free
C_7—1290	C_6—1440
E_6— 890	E_7— 900
F_6—1125	F_7—1160
H_5—1725	H_6—2100
	H_7—1965
I_7—1650	I_6—1600
J_6—1190	J_5—1215
O_5—1100	O_4—1400
O_6—1210	O_7—1200
Q_4— 900	Q_5— 775
S_4—1420	S_5—1220
D_6—1275	D_7— 985
Average 1261	Average 1260

ligature in the one under tension; these loops were so arranged that they acted against each other (fig. 3), so that when the upper one was run over a pulley and a weight attached and a like weight hung on the one below, a pressure equal to the weight used was exerted radially upon the tendril. In order that no injury might be done to the tendril, three lengths of soft cotton twine were placed lengthwise to the tendril, so that they lay between the loops and the tendril; this served well to transmit the pressure to the surface of the tendril. In only a very few cases was the tendril injured by this means. Where such injury occurred, the tendril was thrown out of record. In both cases attachment was made to the tendril slightly below that in the preceding experiment, so that it was just within the proximal third of the tendril, to avoid the contact stimulus as much as possible, since the sensitiveness of the tendril diminishes rapidly toward the base.

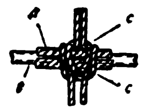


FIG. 3.—*t*, tendril; *c*, loops of cord; *a*, lengths of soft twine to protect tendril from injury.

Weights were added as in the preceding experiment. Breaking strengths of these tendrils are given in table V. Four tendrils in this series were allowed to grow without any contact whatever, to determine the effect of contact-pressure on the basal portion of the tendril, and are included in this table; likewise, one tendril which had a ligature placed similarly to those in the first two columns but without tension or contact-pressure.

These results are very different from those in the last experiment, and seem to verify the inferences made as to the real cause of the unexpected increase in strengthening tissues in the tension-free tendrils in the preceding experiments. That this increase did not take place in the "tension-free" tendrils in the experiments on the middle third is no doubt due to the fact that the part under tension in this case was in the upper or contact portion of the tendril, which is not so sensitive to the tension stimulus. "Tension-free" tendrils show an increase in breaking strength over "free" tendrils, while those under tension show a much greater tensile strength. This must mean that tension in the lower part of the tendrils is effective in giving greater strength to that portion.

only about 10 cm. of mercury was necessary to secure the same amount of radial pressure that is exerted on the contact portion when 20 grams tension is applied to the tendril with the contact portion coiled about a support, due allowance being made for the pressure taken up by the resistance of the rubber tube.

Since, however, in spite of the care taken to secure a close contact between tendril and tube, the amount of pressure which was actually exerted upon the tendril was dependent upon how closely the tendril had coiled about the tube, only relatively high pressures were used, which were for the purpose of determining the effect of pressure alone upon the tendril. A small amount of pressure was applied at first and gradually increased. The tensile strength of the whole tendril was determined in all experiments on the effect of pressure, to see whether an actual increase in the strength of the tendril had occurred. The break occurred, with a very few exceptions, in the middle third.

TABLE VI

PERIOD 28 DAYS

Increased pressure			Normal pressure	
Tendril	Hg. height	Breaking strength	Tendril	Breaking strength
A_2	55 cm.	1085 grams	A_1	785 grams
E_4	30	1775	E_2	975
			E_3	1025
I_2	22	1150	I_1	715
I_3	30	950		
L_2	20	715	L_1	615
L_3	30	960	L_5	625
M_4	45	900		
M_5	30	720	M_3	575
M_6	30	1160		
N_3	30	915	N_5	725
N_4	30	850		
V_3	30	700	V_4	500
Averages		990		727

The breaking strengths as shown in table VI show an undoubted increase in the strength of tendrils with increased radial pressure. That the increase was small in some cases may be due to the failure of the tendril to coil about the tubing securely.

That longitudinal tension may enter into this experiment is quite possible; however, in many tendrils in this experiment where pressure was applied, the contact with the rubber tubing was so close as to permit of a seemingly small amount of longitudinal stretching. That this increase was not in the main due to longitudinal tension may be inferred by a comparison with the results in table VII.

TABLE VII

Period 28 days

Pressure with weight			Contact pressure	
Tendril	Final wt.	Breaking strength	Tendril	Breaking strength
H_1	15 grams	625 grams	H_2	520 grams
K_1	20	600		
K_2	15	685	K_5	740
K_4	5	775		
L_1	20	540		
L_3	20	690	L_2	650
L_4	15	875	L_5	675
M_5	20	875		
M_6	20	600	M_1	600
M_7	15	975		
N_1	20	775		
N_2	20	935	N_5	675
N_3	15	675		
S_1	20	790	S_5	575
S_2	15	890		
Averages		745		634

In order to determine how great a part pressure actually has in the formation of mechanical tissue in tendrils, weights were placed upon the most sensitive part of the tendril, the latter being supported by a small platform suspended from above by a cord. Weights were added exactly the same as when tension was used in the former experiments, and the same length of the tendril was placed under pressure as was calculated to be under pressure in the tension experiments.

The breaking strengths of these tendrils as given in table VII show a slight increase over those tendrils which had contact alone. We infer from this that the additional radial pressure caused by an amount of tension equal to 20 grams does not greatly increase

the strength of the tendril. This may be explained by the supposition that a weight of 20 grams does not exert a pressure much greater than is caused by the contraction of the contact portion of the tendril when coiled about a support.

Ligatures were also tied about tendrils in different regions to determine the effect of contact in a more and in a less sensitive part of the tendril. The effect of these ligatures in regions *a* and *b*, respectively, upon the breaking strength is shown in table VIII; *a* was about one-third the length of the whole tendril from the apex, and *b* the same distance from the base of the tendril.

TABLE VIII

PERIOD 32 DAYS

Ligature at *a*		Ligature at *b*	
Tendril	Breaking strength	Tendril	Breaking strength
B_7	230 grams	H_8	590 grams
D_8	550	H_{10}	310
D_9	510	H_{11}	160
I_5	490	K_4	140
I_6	650	K_5	225
J_2	650	K_6	260
J_4	700		
J_5	665		
L_3	510		
M_3	600		
M_4	750		
Averages	573		281

These results show that a ligature placed in a more sensitive region (*a*) calls forth a greater formation of mechanical tissue than when placed in a less sensitive region (*b*). This accords with the former inferences made in experiments on the middle third and basal third.

RESULTS IN BREAKING STRENGTH

The following conclusions may be deduced from the foregoing results in breaking strength of tendrils:

1. Contact alone plays an important part in giving strength to the tendril.

2. When contact is increased by pressure, a further increase in the strength of the tendril is produced.

3. When the factor of tension is added to that of contact, a still greater strength results to the tendril.

ANATOMICAL STUDY

1. *General anatomy of the Passiflora tendril.*—A cross-section of a tendril of *Passiflora caerulea*, in accordance with the observations of MacDougal (13) and Worgitzky (26), reveals the following tissues, beginning at the outside: epidermis, collenchyma, thin-walled parenchyma, bast, xylem (which forms a complete ring, due to secondary growth), and in the center pith. In mature tendrils the pith entirely fills the central part except in the basal portion, where there is a central cavity within the pith. The walls of the xylem and bast are much thickened, and so are (as Worgitzky has noted, p. 34) the walls of the pith. The xylem becomes lignified, also the bast somewhat, and, as MacDougal observed, lignification extends to the pith also.

At the base the arrangement of tissues is very nearly radial, but in the portion in contact a marked dorsiventrality is seen, which is due principally to the development of the xylem to a much greater extent on the side in contact. A section midway between the apex and base of the tendril shows a slight dorsiventrality, a somewhat greater amount of xylem being formed on the concave side.

2. *Study of sections; experiments on entire tendril (free, with contact alone, and with contact and tension).*—Sections were made through the middle of the tendrils, as this was found to be the place at which the break invariably occurred in these experiments. Tendrils as near as possible to the average breaking strength were taken for sectioning. A comparison of sections reveals the following.

The mechanical tissue of the free tendril is limited to a small area of xylem on the concave side, and only the four primary bundles on the opposite side. The xylem cells are quite thin-walled compared with the xylem of the other tendrils in this experiment, and the primary bundles of the opposite side are

composed of two or three slightly thickened vessels. In this region only a few bast fibers are present, which are very small; very little pith is present, which lines a central cavity. Toward the base a complete ring of thin-walled xylem and pith is formed.

Sections of those tendrils under contact and under tension show the normal complete ring of mechanical tissue and central thin-walled pith. At the first examination of these sections, little difference could be seen in structure or areas of mechanical tissue, and camera sketches show no difference in thickness of walls of the xylem, though the greater part of those under tension had a tensile strength 50 per cent higher than those with contact alone. A closer examination of the sections with the aid of microphotographs and camera sketches shows that while the xylem areas are approximately the same in both, in the one where tension had been introduced the walls of the pith cells have become much thickened, while in the one with contact alone they are quite thin-walled. This thickening of walls takes place usually throughout the whole area of the pith of the tendril under tension, while in the one which had been under contact alone the pith is thin-walled throughout. It is worthy of note also that in sectioning, the ones under tension were much harder to cut through, which is no doubt due to a difference in density of cell walls.

3. *Study of sections; experiments on middle third.*—Examination of sections of those tendrils where the middle third was (1) with and (2) without tension shows the diameter of mechanical tissue to be much greater in the latter, which accounts for the greater outside diameter usually found in these tendrils. This seemingly greater area of mechanical tissue in the tendril grasping a support but not under tension is somewhat surprising when we consider that those under tension had a breaking strength nearly 50 per cent higher. This increased strength with tension is at least partly accounted for by the fact that the pith walls in the tension-tendril are thickened (very similarly to those in the preceding experiment under tension), while in the one not under tension all the pith is thin-walled. In order to be certain that this thickening of the pith is constant with those under tension, sections of more than 30 tendrils in this experiment were studied

and compared, each being labeled so that it could not be told during the examination which was from a tension and which from a tension-free tendril. In every case it was possible to decide with certainty which one had been under tension from the appearance of the pith, and each decision was later verified by referring to the record. The walls of the pith were in most cases thickened in a marked manner to the very center. Measurements with a planimeter show the tension-free tendril to have the greater area of xylem, while the tension-tendril has the greater amount of mechanical tissue when thick-walled pith is included. Comparative areas were found to be as follows:

	Xylem	Pith (thick-walled)	Total
Under tension	2.61	2.78	5.39
Tension-free	4.51	....	4.51

In these experiments, as in the others where tension was used, a marked characteristic of the sections of tension-free tendrils was that the pith was found more or less displaced by the process of sectioning, while in those from tension-tendrils the pith held its shape as if firm.

In all these tendrils it was noted that tendrils which had been under tension were more rigid and much harder to cut through than those free of tension, as noted in the preceding experiments.

Sections were taken also through the basal third of these same tendrils. A close resemblance was found between sections in these two regions (middle and base) in the same tendril. In the basal part of the tendril in which the middle third had been under tension, the diameter of the mechanical tissue is smaller and the pith thick-walled throughout, while in the tendril tension-free the pith is very thin-walled in the corresponding region. This shows remarkably how the stimulus for growth may be transferred through the tissues to a part which has not received the stimulus directly, since the basal part in neither case in these experiments was under tension.

4. *Study of sections; experiments on basal third.*—Sections of tendrils in which the basal third was tested were studied with the

view especially to ascertaining the cause of the difference in results obtained in breaking strength under the two different methods of experimentation (see tables IV and V). Sections of tendrils in the first set of experiments (where two ligatures were used in the one not under tension) showed the ring of mechanical tissue in the one not under tension to have a greater outside diameter than that in the one under tension. Xylem and thickened pith are present in both tension and tension-free tendrils. A well marked difference could be observed, however, between the amounts of xylem and thickened pith in the two sets of tendrils. In the one not under tension xylem was present in greater quantity than in the one which had been under tension, while in the tension-tendril thickened pith was in much greater quantity than in the one without tension. In a typical tendril the comparative amounts of xylem and thick-walled pith were as follows:

	Xylem	Pith thick-walled	Pith thin-walled	Total mechanical tissue
Under tension	6.0	4.7	(1.7)	10.7
Tension-free	7.2	1.8	(3.6)	9.0

The fact that, nothwithstanding the smaller area of mechanical tissue, the breaking strength of the ones not under tension was practically the same as in those under tension, is no doubt due to the fact that much of the thick-walled pith in the tension-tendril does not possess as thick walls as does the xylem; hence does not give as much strength to the tendril as does the latter. An examination of sections in the second series of experiments on the basal third, where contact-pressure was applied to the tension-free tendril by means of two loops of cord pulling against each other, shows a very different appearance from that just described when tension and tension-free tendrils are compared. In this case the area of xylem is practically the same in both, being about equal to the amount found in those under tension in the above experiments on the basal third; in the ones not under tension the pith is thin-walled throughout, is small in amount, and has a large cavity in the center; in the ones under tension the pith is much

thickened, is larger in amount than in the last, and the central cavity is much smaller.

If we now compare the structure of the tendrils in the two methods of experimentation, it becomes very evident that the additional amount of xylem in the tension-free tendrils (as compared to the tension-tendrils) of the first set is due to the extra contact-pressure introduced, and the thick-walled pith found in the same tendrils, which has not before appeared in tendrils except when tension was introduced, is due to the stimulus of tension conducted to the basal part from the portion in tension between the two ligatures. That this thickening of the pith which was caused by only a small portion of the tendril being under tension did not appear in the former experiments on the middle third of the tendril is no doubt due to the fact that the tension in the latter case was in the contact portion of the tendril, which is not so sensitive to the stimulus of tension as is the lower two-thirds of the tendril.

5. *Study of sections; experiments on contact portion.*—Examination of sections through the contact region of tendrils which had been put under (comparatively) great pressure by a column of mercury failed to detect any difference in anatomical structure when compared with those which had been in contact only. Sections through the middle of the tendrils, however, where there was no tension and where the break usually occurred, show marked differences between the two sets of tendrils in the amount of xylem present. The area of xylem in the ones which had been under pressure, in an average tendril, was approximately twice as great as the area of xylem in the ones which had been in contact only. No differences in the pith could be detected; it was thin-walled alike in both sets of tendrils.

In those cases where a pressure of 20 grams was obtained by laying a weight on the tendril, no difference could be observed between these tendrils and those under mere contact, though the former had a slightly greater average breaking strength. Both had the usual ring of xylem and the pith was thin-walled.

Sections were not made of tendrils which were ligatured in different regions.

SUMMARY AND CONCLUSIONS

These changes in structure under changing conditions which were observed upon a number of tendrils in each condition and were found constant in each case, almost without exception, have but one meaning to the writer. In experiments where tension was introduced, the marked increase in thickness of pith walls, which was found only when the factor of tension was present, can be explained only by the theory that this thickening is due to the longitudinal pull on the tendril, by which the tensile strength of the tendril is increased.

That pith may serve as mechanical tissue is a thing for which no evidence has heretofore been offered. DEBARY says (*Comp. anat.*, p. 533):

> The only demonstrable change in the pith during the phenomena of secondary growth is that it sooner or later, rapidly or slowly, dies off and dries up. The possibility of a change in the pith caused directly by the growth in thickness is not, indeed, excluded a priori. For . . . . the increasing pressure . . . . exercised on the pith [by the xylem] may lead to anatomical changes in the latter. In what cases and in what form such changes may possibly take place are questions which have not been investigated, and to the solution of which there is scarcely any safe clue; the possibilities will not be discussed here.

WORGITZKY noted a thickening of the walls of the pith in the tendrils of *Passiflora caerulea*, *P. triloba*, and *P. quadrangularis*, "after a support had been securely grasped." He also adds "the purpose or cause of this was not found"; and MACDOUGAL noted that lignification extended to the pith in the basal part of tendrils of *P. caerulea*.

In view of the results of observations and experiments presented in this paper, I maintain that this thickening of the walls of the pith cells in *Passiflora caerulea* is an adaptation, where tension acts as an irritation-stimulus, for producing greater tensile strength to the tendril where needed.

In the series of experiments on the contact portion, the great increase in xylem below the part in contact, accompanying the increased pressure, leads to the conclusion that contact-pressure has a marked effect upon the structure of the tendril. That a pressure of 20 grams does not cause a decided increase in xylem

may be explained if we assume that the pressure exerted on the support by the coils of the part in contact which contract after grasping the support is equal to 20 grams for the whole area in contact. No constant change could be noted in the amount of bast present under these varying conditions, except that very little could be found in the free tendrils. As the bast plays only a comparatively small part in the *Passiflora* tendril, this tissue was not taken into consideration.

The conclusion from these anatomical studies on *Passiflora* can only be that contact-pressure causes a greater formation of xylem in the tendril, while longitudinal tension causes a thickening of the walls of the pith whereby greater tensile strength is secured.

General conclusions

To return to the problem of the present paper (as given in the introduction), my conclusion in regard to *Passiflora caerulea* is that those tendrils which function to support the plant, that is, that are under the influence of contact and tension, possess a greater breaking strength than those which have grasped no support (see table I).

The cause of this greatly increased strength, as shown by the experiments on the middle third, basal third, and contact portion, and a study of sections of the same, is clearly due to a combination of the two factors contact and tension, the cells of the xylem being increased both in number and in thickness of walls by the former stimulus, and the walls of the pith much thickened by the latter. Comparing the values of these two factors in the formation of mechanical tissue in the *Passiflora* tendril, I conclude that contact plays by far the most important part, though the strength of the tendril may be still more increased (even 50 per cent) by the additional factor of tension.

As to the influence of contact upon the formation of tissues, we have had a large number of observations, not only in regard to tendrils, but also in regard to plant tissues in general.

That tension also may act as a stimulus, and that thereby stronger tissues are built up in the plant, has been shown by the experiments of BORDNER (3); this is substantiated by the observa-

tions and experiments presented in this paper. This accords with the observations of HEGLER (**8**) that the retarding effect of tension is closely related to the daily periodicity of growth in length, which seems to show that tension acts as a true stimulus upon the plant cell. As to the exact method by which this increase and strengthening of tissue takes place we are unable to say, since we know very little, as yet, of the nature of the changes taking place in the cell and especially in the cell wall, under the influence of tension.

It seems not unlikely that this increased growth is due to increased hydrostatic pressure in the cell, since HEGLER found a higher hydrostatic pressure in plants which had been under tension than in plants growing normally (**7**, p. 416).

The state of tension in which the cell wall might be, may act as an irritation-stimulus for the laying down of more tissues either by apposition or intussusception; here, however, we should have to assume the cell membrane (at least in part) to be composed of living protoplasm, for which assumption we have no well founded evidence (see PFEFFER **18** [EWART transl.], **1**:485).

As to why this thickening in *Passiflora* did not occur in the xylem also under the influence of tension, we are unable to say; this difference in response is probably due to fundamental differences in these tissues.

This investigation was conducted at the University of Michigan under the direction of Professor F. C. NEWCOMBE, to whom I wish to express my sincere thanks for his kindly interest and helpful suggestions.

WASHINGTON, D.C.

LITERATURE CITED

1. BALL, O. M., Der Einfluss von Zug auf die Ausbildung von Festigungsgewebe. Jahrb. Wiss. Bot. **39**:305. 1904.
2. BARANETSKY, J., Die tägliche Periodizität im Längenwachstum der Stengel. Mém. Acad. St. Pétersbourg **27**: no. 2. 1879.
3. BORDNER, J. S., The influence of traction on the formation of mechanical tissue in stems. BOT. GAZ. **48**:251. 1909.
4. CHAMBERLAIN, C. J., Methods in plant histology. Chicago. 1901.

5. DARWIN, CHARLES, Movements and habits of climbing plants. 1876. pp. 48–51; Jour. Linn. Soc. London 9: 1867; see review in SARGENT, Scientific papers of Asa Gray 1:176. 1889.
6. DE VRIES, HUGO, Arbeit Bot. Inst. Würzburg 1:3305. 1873.
7. FITTING, HANS, Weitere Untersuchungen zur Physiologie der Ranken. Jahrb. Wiss. Bot. 39:424. 1904.
8. HEGLER, R., Ueber den Einfluss des mechanischen Zugs auf das Wachstum der Pflanzen. COHN's Beiträge Biol. Pflanz. 6:383. 1893.
9. ———, Reported by PFEFFER (which see).
10. HIBBARD, R. P., The influence of tension on the formation of mechanical tissue in plants. BOT. GAZ. 43:361. 1907.
11. KELLER, H., Ueber den Einfluss von Belastung und Lage auf die Ausbildung des Gewebes in Fruchtstielen. Inaug. Diss. Kiel. 1896.
12. KNIGHT, T. A., Phil. Trans. Roy. Soc. London, pp. 280–283. 1803.
13. MACDOUGAL, D. T., Mechanism of curvature of tendrils. Ann. Botany 10:373. 1896.
14. MÜLLER, O., Unters. über die Ranken d. Cucurbitaceen. COHN's Beiträge Biol. Pflanz. 4:97. 1887.
15. NEWCOMBE, F. C., Regulatory formation of mechanical tissue. BOT. GAZ. 20:441. 1895.
16. PENNINGTON, L. H., The effect of longitudinal compression upon the production of mechanical tissue in stems. BOT. GAZ. 50:257. 1910.
17. PFEFFER, W., R. HEGLER's Untersuchungen über den Einfluss von Zugkräften auf die Festigkeit und die Ausbildung mechanischer Gewebe in Pflanzen. Ber. König. Sächs. Gesell. Wiss. Leipzig 43:638. 1891.
18. ———, Pflanzenphysiologie 2^2: Leipzig. 1897.
19. RICHTER, J., Ueber Reactionen der Characeen auf äussere Einflüsse. Flora 78:419. 1894.
20. SACHS, J., Textbook of botany. 4th ed. 1874. "The mechanics of growth."
21. SCHOLTZ, M., Ueber den Einfluss von Dehnung auf das Längenwachstum der Pflanzen. COHN's Beiträge Biol. Pflanz. 4:323. 1887.
22. TREUB, M., Sur une nouvelle catégorie des plants grimpantes. Ann. Jard. Bot. Buitenzorg 3:65. 1882.
23. VÖCHTING, H., Zur experimentellen Anatomie. Nachricht König. Gesells. Wiss. Göttingen 38:278. 1902.
24. VON DERSCHAU, M., Der Einfluss von Kontakt und Zug auf rankende Blattstiele. Inaug. Diss. Leipzig. 1893.
25. WIEDERSHEIM, W., Ueber den Einfluss der Belastung auf die Ausbildung von Holz- und Bastkörper bei Trauerbäumen. Jahrb. Wiss. Bot. 38:41. 1903.
26. WORGITZKY, G., Vergleichende Anatomie der Ranken. Flora 69:2. 1887.

A COMPARISON OF THE RATES OF EVAPORATION IN CERTAIN ASSOCIATIONS IN CENTRAL ILLINOIS[1]

HENRY ALLAN GLEASON AND FRANK CALEB GATES

(WITH SIX FIGURES)

During the session of the Biological Summer School of the University of Illinois, held at Havana, Ill., during June and July 1910, a series of measurements of the relative rates of evaporation within certain plant associations was made. In view of the growing interest in the study of evaporation and its relation to vegetation, the results obtained are here presented.

The greater part of our knowledge of evaporation in relation to vegetation has been given to us through the work of LIVINGSTON and TRANSEAU. One of the most suggestive papers is that of TRANSEAU,[2] in which he determined the relative rates of evaporation for a number of habitats about Cold Spring Harbor, Long Island, N.Y. He has summarized his results in a diagram which clearly shows the marked difference in the amount of evaporation in areas close to each other but differently vegetated. While TRANSEAU worked with habitats, as he expresses it, in the work at Havana certain definite plant associations were selected in which to determine the rate of evaporation.

Havana is located on the east bank of the Illinois River in central Illinois. The climate may be briefly characterized by the following statements: an average temperature during June and July of about 24° C., with warm nights and hot days, and a yearly rainfall of about 90 cm., of which considerably more than half falls during the growing season. Strong winds are frequent, as is usually the case in the central states. Except on the alluvial river bottoms, the soil of the area is sandy with a slight admixture of humus. Most of the area was originally occupied by associations of the Prairie

[1] Contribution no. 125 from the Botanical Laboratory of the University of Michigan.

[2] TRANSEAU, E. N., The relation of plant societies to evaporation. BOT. GAZ. 45:217–231. 1908.

Province, but the climatic dominance of the associations of the Deciduous Forest Province is now gradually asserting itself wherever conditions are not interfered with by man. The climax type of vegetation for this part of Illinois, the *Acer saccharum* association, does not occur in the immediate vicinity, although it is present on clay and loess bluffs on the opposite side of the river.

The principal object of the investigation was the determination of the relative amounts of evaporation in certain well marked associations whose successional relations were clearly evident, in order to correlate the phenomena of succession and evaporation. A minor object was the comparison of evaporation in two areas with the same dominant vegetation, but with different secondary species. The results obtained were even more striking than had been anticipated.

The atmometers used were porous clay tubes, of the model recommended by TRANSEAU, about 30 cm. long and 2 cm. in diameter. The tubes were inserted into bottles through holes in the corks, and were then sealed with red sealing wax to prevent the entrance of rainwater and the loss of water by evaporation. A small S-shaped groove on the side of the cork permitted the equalization of the atmospheric pressure within the bottle. Reading the instruments immediately before and after heavy rains indicated that the arrangement was water-tight. The instruments were filled with distilled water, and to each 250 cc. was added one drop of formalin to prevent the growth of organisms. According to LIVINGSTON[3] the addition of formalin is not recommended in studies of absolute values of evaporation. Since this study was concerned with relative values only, and since all the instruments were treated alike, the slight effect of formalin is without significance. The instruments were set up and allowed to run for three weeks before the field records were taken, to insure the thorough saturation of the clay tubes. Each bottle was marked just below the cork, and was refilled by pouring in water from a graduate up to the mark. The readings were estimated to be correct within 0.5 cc. All the instruments were exposed together in the open air for 93 hours for standardization. Eleven instruments were then exposed in the association selected, while a twelfth, arbitrarily chosen as the stand-

[3] Plant World 13:118. 1910.

ard, remained in its original location. Readings in the field were continued for 23 days, and then all the instruments were again standardized for 93 hours in the original location. Readings of the standard were taken daily, while those in the field were read at intervals of one to four days. Since the purpose of the work called for the total amount of evaporation rather than the daily fluctuations, the observed amounts of evaporation from each instrument were added, and the total amounts reduced to terms of the standard instrument by multiplying by the factor obtained in the two standardizations. The results are therefore directly comparable, and have been plotted in the accompanying diagram (fig. 6). Since they are not absolute values, they have been expressed in terms of the evaporation from the standard instrument, which is here designated 1.00.

Two atmometers were located in each of five distinct associations, and one other was set up on the sandy beach of Quiver Lake. Four of the associations were in sandy soil, and their vegetation has been described in detail by GLEASON.[4] A brief description of the vegetation and the successional relations of the associations, however, may be given here.

The standard.—During standardization the atmometers were placed on the ground in the Chautauqua Park athletic field, and the standard instrument was kept there during the whole period of observation. This field was formed by leveling the sandy ground after cutting off the mixed forest association which covered it. It was bordered by a cultivated field on the east, and was surrounded on the other three sides by forest at a distance of 50–100 m. from the atmometers. The field was partly covered by weeds, of which the following were the most abundant: *Erigeron canadensis*, *Mollugo verticillata*, *Eragrostis Purshii*, *Erigeron divaricatus*, *Verbena stricta*, *Erigeron annuus*, *Cenchrus carolinianus*, and a few other grasses. The atmometers were placed in the center of an area cleared of the taller weeds for a radius of about one meter (fig. 1).

The river bank.—One atmometer was maintained on the sandy eastern bank of Quiver Lake, at a height which corresponds to a

[4] GLEASON, H. A., The vegetation of the inland sand deposits of Illinois. Bull. Ill. State Lab. Nat. Hist. 9:23–174. *figs. 6. pls. 20.* 1910.

reading of 15 feet above the zero of the Havana gauge, located about 2.5 km. south. The lake has a continuous connection with the Illinois River, forming an expanse of water about 400 m. wide. During the course of the experiment the river fell from 12 to 7.8 feet on the Havana gauge. The location of the atmometer was selected to show the evaporation from an open surface near the

FIG. 1.—Atmometers in process of standardization, June 22, 1910; photograph by F. C. GATES.

water. The ground is sandy and for the most part without vegetation because of its regular inundation during high water in the river. The plants that occur along the beach are mostly sand plants, such as *Sporobolus cryptandrus*, *Cenchrus carolinianus*, and *Opuntia Rafinesquii*. There are some relics from the mixed forest above, as *Clematis Pitcheri*, and numerous xerophytic weeds, as *Melilotus alba*. A few trees still grow at the water's edge, but most of the original shore vegetation has succumbed to the effect of the higher average level of the water since the opening of the Chicago

Drainage Canal. The evaporation from this atmometer was very pronounced during the day, but was much lower at night. Sometimes virtually no nocturnal evaporation was indicated, while on the athletic field, about 200 m. inland and separated from the river by a forested dune, the evaporation was quite noticeable.

The bottom-lands.—The bottom-lands immediately across the river show plainly the results of the persistent high water during the last few years. The low banks and islands between the numerous lakes are still mostly covered with trees, but they are gradually being killed. A marginal zone of *Salix longifolia* represents the *Salix-Cephalanthus* association, while in the interior or highest parts of the islands a few maples, *Acer saccharinum*, occur, showing the former presence of the *Ulmus-Acer* association. A few pecan trees, *Carya illinoensis*, are present, but other tree species are rare. The ground is submerged during the greater part of the year. If emergence occurs during the summer, the surface is in a few weeks thickly covered with a growth of weeds, of which the most abundant are *Xanthium commune*, species of *Aster*, and other composites, and with numerous seedlings of willow and maple, none of which, however, survives the following winter. One atmometer was placed in a large rotten willow stump, about 6 m. from the river bank and about 2 m. above the surface of the mud. When first located, the station was covered half a meter deep with water. Another instrument was stationed in a maple stump, 1.7 m. above the mud, and about 8 m. from the river (fig. 2). Since the maple leaves were more nearly confined to the upper parts of the trees, while the willows were leafy almost to the ground, the better circulation of air permitted a greater evaporation under the maple trees.

The bunch-grass association.—Of the several consocies of the bunch-grass association occurring in the region, two adjacent ones were selected, characterized respectively by *Eragrostis trichodes* and *Leptoloma cognatum*. The former of these is the more stable, and consists chiefly of well defined bunches of *Eragrostis* spaced about 2–4 dm. apart. Other less conspicuous or less abundant grasses occur also, particularly *Andropogon furcatus*, *Leptoloma cognatum*, *Sorghastrum nutans*, and *Paspalum setaceum*, with a few plants of

other species. Scattered among the grasses are plants of several secondary species which fill the spaces between the bunches and give the area the appearance of a closed association. The more prominent of these are *Lespedeza capitata*, *Opuntia Rafinesquii*, *Crotonopsis linearis*, *Ambrosia psilostachya*, *Oenothera rhombipetala*, *Lepidium virginicum*, *Krigia caroliniana*, *Cyperus Schweinitzii*,

FIG. 2.—The center of a willow island, showing atmometer no. 1 on a maple stump, July 9, 1910; photograph by F. C. GATES.

Specularia perfoliata, *Croton glandulosus*, *Erigeron canadensis*, *Commelina virginica*, *Monarda punctata*, *Callirhoe triangulata*, *Carex Muhlenbergii*, and *Erigeron strigosus*.

The *Leptoloma* consocies, which is very abundantly represented in this region, is a less stable type of bunch-grass. The dominant species, *Leptoloma cognatum*, does not form bunches as well defined as those of *Eragrostis trichodes*, but with its spreading habit and irregular bunches occupies a larger proportion of the area. With it are associated a few other grasses, especially *Panicum pseudo-*

pubescens, *Cenchrus carolinianus*, *Sporobolus cryptandrus*, and *Bouteloua hirsuta*, with less of *Paspalum setaceum* and *Andropogon scoparius*. The secondary species are not numerous, but a few species are so conspicuous at certain seasons of the year that they make distinct aspects. The *Oenothera rhombipetala* aspect dominated during the period in which this experiment was conducted. The most important secondary species are *Opuntia Rafinesquii*, *Lepidium virginicum*, *Ambrosia psilostachya*, *Tephrosia virginiana*, *Chrysopsis villosa*, *Monarda punctata*, *Croton glandulosus*, *Oenothera rhombipetala*, *Cyperus Schweinitzii*, *Tradescantia reflexa*, *Specularia perfoliata*, *Lithospermum Gmelini*, *Petalostemum purpureum*, *Draba caroliniana*, *Euphorbia Geyeri*, *Lespedeza capitata*, *Krigia caroliniana*, *Cassia Chamaecrista*, *Pentstemon hirsutus*, *Antennaria* sp., and *Aster sericeus*. The atmometers in these two consocies were about 15 m. apart.

The blowouts.—The blowouts are excavations in the mobile sand caused by the action of wind. In this region nearly all of them are surrounded by the bunch-grass prairie. The sand is virtually free from vegetation except for a few species, such as *Acerates viridiflora*, var. *lanceolata*, *Cristatella Jamesii*, and *Aristida tuberculosa*, which find here their preferred habitat. The dry surface layers of the sand are blown by every wind, and become very hot on sunny days. One atmometer was placed in the bottom of the complex known as the Devil's Hole, 3 km. east of Havana, and another half-way up its lee slope toward the east (fig. 3).

The Quercus velutina association.—The first forest association to appear on the sand in this region is characterized by *Quercus velutina* and *Q. marilandica*. Of the two, the former is usually more abundant and better developed. In typical situations other species of trees are seldom present. In general, *Q. marilandica* tends to occupy the poorer soil, and is more frequently the first to appear on cleared or lumbered land, but *Q. velutina* seems to be more persistent and better able to hold its own. The presence of trees of *Carya cordiformis* may indicate an incipient succession of the mixed forest association. Actual count of the trees in the vicinity of one atmometer showed that 57 per cent of the old trees were *Q. velutina*, 42 per cent *Q. marilandica*, and 1 per cent *Carya*

cordiformis. In the typical areas of this association, there are neither vines nor shrubs, with the exception of some shrubs remaining as relics from the prairie, even though the seeds are already present in the sand beneath the trees. The presence of *Psedera quinquefolia* and other vines in some places is accordingly considered an indication of the approaching succession of the mixed forest

FIG. 3.—A blowout near the station of atmometer no. 8, July 1910; photograph by ARTHUR G. VESTAL.

association. The shrubby growth consists largely of the young trees of the dominant species, together with *Rhus canadensis*, var. *illinoensis*, and *Ceanothus americanus*, relics from the bunch-grass. The herbaceous vegetation but sparsely covers the ground, although the number of species represented is usually large. The most common and typical are *Tradescantia reflexa*, *Amorpha canescens*, *Euphorbia corollata*, *Smilacina stellata*, *Phlox bifida*, *Verbascum Thapsus*, *Monarda fistulosa*, *Lithospermum Gmelini*, *Aster azureus*, *Rudbeckia hirta*, *Lespedeza capitata*, *Pentstemon hirsutus*, *Asclepias tuberosa*, *Tephrosia virginiana*, and *Rosa humilis*. The soil is sand

to within a few centimeters of the surface, which is covered with a layer of dead but undecayed leaves. Two atmometers were maintained in woods of this type about 500 m. from the bunch-grass and blowouts. One of them was in a typical area of the vegetation (fig. 4), and the other in an area in which there were numerous young trees of *Carya cordiformis*.

FIG. 4.—Interior of *Quercus velutina* association, showing atmometer no. 7, July 9, 1910; photograph by F. C. GATES.

The mixed forest association.—In the mixed forest more than half of the trees are of species typical of the *Quercus velutina* association which has preceded it. In this particular area, the oldest trees are without exception *Quercus velutina*, while near the edge there are some large *Q. marilandica*. There are also numerous young trees of *Carya cordiformis*, which are nearly as large as the more slowly growing oaks. Scattered among the individuals of these three species are a few trees of *Gymnocladus dioica* and *Celtis occidentalis*, the latter only near the margin. An actual count of

the trees near the atmometer gave the following results: *Carya cordiformis*, 62.5 per cent; *Quercus marilandica*, 19.2 per cent; *Q. velutina*, 14.3 per cent; *Celtis occidentalis*, *Gymnocladus dioica*, and *Quercus rubra*, each 1 per cent. The proportion of the young trees, however, is very different. Between 80 and 90 per cent of them are *Carya cordiformis*. They dominate in every clearing, although occasionally they are accompanied by a few young trees of *Quercus velutina*. Young trees of *Q. marilandica* are not at all plentiful and occur only at the edges. The luxuriance of the growth of vines is the most prominent feature of the change from the *Quercus velutina* association. Nearly everywhere in the mixed forest vines are the conspicuous ground cover. This is never true of the typical *Quercus velutina* association. Most prominent of these is *Psedera quinquefolia*, which not only carpets the ground with green, but also climbs to a considerable height. More noticeable as climbers, however, are *Celastrus scandens* and *Vitis vulpina*. Shrubs are prominent only near the margin of the association, although a few species are scattered throughout. The commoner species of the herbaceous vegetation are *Scrophularia leporella*, *Anychia canadensis*, *Parietaria pennsylvanica*, *Hedeoma pulegioides*, *Asclepias phytolaccoides*, *Galium circaezans*, *Aquilegia canadensis*, *Galium pilosum*, *Silene stellata*, and *Cacalia atriplicifolia*. Two atmometers were maintained in this association. One was located near the margin of the grove, while the other (fig. 5) was near the center.

From an inspection of the data given in the diagram it is seen that the bunch-grass, the blowout, the *Quercus velutina*, and the mixed forest associations all show noticeably different amounts of evaporation. The instruments in these associations were located within half a kilometer of each other, in a region of comparatively uniform topography. The variation in the physical factors of the environment is not sufficient to explain the wide variation in the amount of evaporation. Accordingly the vegetation, which is the most variable factor of the environment, appears to be the essential factor in determining the evaporation rate. This, however, is accomplished indirectly, since vegetation influences evaporation chiefly through the control or modification of the wind, the temperature, and the humidity, all of which affect the evaporation

directly. The diagram shows also that those associations which stand high genetically have a lower evaporation rate than those genetically lower in the successional series.

This relation between succession and evaporation is best shown in the sand dune habitats, where four sets of atmometers were maintained. The original vegetation there is the bunch-grass

FIG. 5.—Interior of the mixed forest association, showing atmometer no. 11, July 9, 1910; photograph by F. C. GATES.

association, but under certain conditions portions of the association may be destroyed by wind action, resulting in open areas of bare sand, the blowouts. The present blowouts are all of secondary origin, but their environment and vegetation probably represent the primitive condition of the region, shortly after its emergence from the glacial Illinois River. In these blowouts the highest evaporation occurs. The blowout is eventually revegetated by bunch-grass, during which process two or more consocies of the bunch-grass association appear. The *Leptoloma cognatum* consocies

is usually the earliest one to develop, and later is followed by the *Eragrostis trichodes* consocies. The latter, representing the higher development of the association, has an evaporation rate which is 88 per cent of the lower type. In both cases the amount of evaporation from the bunch-grass is lower than that from the blowout, although the four atmometers were less than 100 m. apart.

The difference in the rate of evaporation in the bunch-grass and *Quercus velutina* associations is much more marked. Young oak trees in different stages of development are present in the former

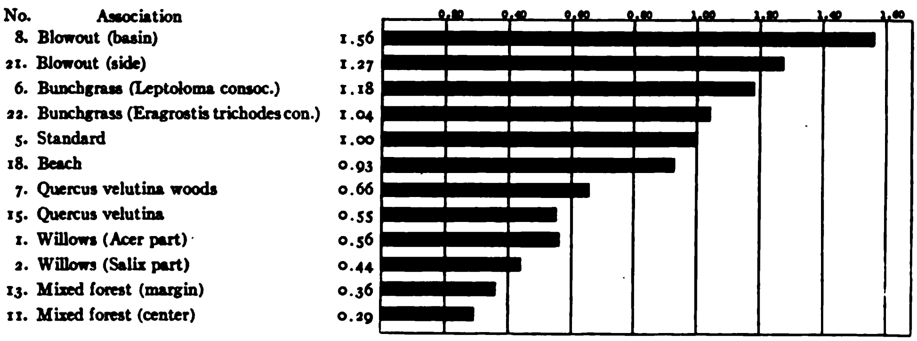


FIG. 6.—Diagram showing relative amounts of evaporation in the different stations.

association, clearly demonstrating that they are capable of withstanding the relatively high prairie rate of evaporation. With their growth to maturity, and the consequent succession of the bunch-grass by the forest, the evaporation beneath them is steadily diminished, until it becomes about 55 per cent of that of the normal bunch-grass. Atmometer no. 7 was placed in a typical part of the *Quercus velutina* association (fig. 4).

With the increase in the age and density of the forest cover, the evaporation beneath it is still further reduced. Eventually the succession of the mixed forest association begins, and the first indication is usually shown by the presence of *Psedera quinquefolia* and *Celastrus scandens*. Atmometer no. 15 was located in such a place, and the diagram shows a reduction in the rate of evaporation from 0.66 to 0.55, in terms of the standard. The reduction is still greater in the typical mixed forest, represented by instruments

11 and 13, the latter of which was placed near the border of the association, while the former was in the center. With the establishment of the mixed forest association the sand area reaches the present culmination of the successional series. Throughout this series the amount of evaporation has steadily decreased, reaching its lowest rate in the association genetically highest.

Actual observation shows that the succession of the bunch-grass by the *Quercus velutina* association begins in the normal association, where the rate of evaporation is high. It also shows that members of the mixed forest association appear in the *Quercus velutina* association while the evaporation rate there is still relatively high. In both cases the development of the association reduces the evaporation. Succession, therefore, does not depend upon evaporation; it is a cause rather than an effect.

The other records shown in the diagram are not to be placed in this genetic series. Sufficient instruments were not at hand, nor does this particular locality give the opportunity for investigation in the series of associations beginning with the open water and ending with bottom-land forests. Nevertheless, one or two points are brought out, notably that the evaporation on the open sand of the river beach is not nearly so great as that from the open sand of a blowout. The river is here a most important factor, tending to reduce the extremes of temperature during the day, and maintaining a relatively high humidity during the night. Evaporation from the willow and maple islands was greater than from the mixed forest, although the latter grew in dry upland sand, and the former in mud, during part of the experiment covered and at all times surrounded by large bodies of water. This is simply another instance indicating that the vegetation is of greater importance than the physical environment in controlling evaporation.

Conclusions and summary

1. Since proper conditions for maintaining an absolute standard were lacking, the results were all calculated on the basis of one instrument arbitrarily chosen as a standard, and are represented in relative terms only.

2. Differences in the amount of evaporation in various associations are due chiefly to the nature of the vegetation, which by its size and density controls the evaporation beneath it.

3. The observations indicate that successions between associations are not caused by any conditions of evaporation.

4. The more primitive associations have the higher rates of evaporation, while those most nearly like the climax type have the lowest rates. This is true not only for the forest associations, in which low evaporation is expected, but also for the prairie associations, which are correlated with an arid climate and consequently high climatic evaporation.

The standardization and field observation of the atmometers and the evaluation of the relative rates of evaporation were managed entirely by the junior author; for all other statements both authors are responsible.

UNIVERSITY OF MICHIGAN
ANN ARBOR, MICH.

A STUDY OF TARGIONIA HYPOPHYLLA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 156

HERMANN DEUTSCH

(WITH THIRTEEN FIGURES)

Considerable work has already been done on the morphology of *Targionia hypophylla*, LEITGEB (1) and CAMPBELL (2) being foremost among the investigators. Recently CAVERS (3) also published a paper on the same species; but with all this there still remains some little ground which has not been covered at all, as well as some which has been covered but superficially. These points it is the aim of this paper to try to clear up.

The material for this study was collected in 1908 by Drs. BARNES and LAND along the steep slopes of the canyon of the Rio Santiago in western Mexico, and also on the eastern slope of Mt. Orizaba. In both regions it was found only at an altitude of 1500 meters.

Gametophyte body

The thallus in this group is about as complex as in any of the Marchantiales. This statement is not based on any one of the several characters that usually distinguish a thallus as simple or complex, but on an average of the total amount of differentiation and complexity present.

In the first place, the thallus is formed by the segmentation of a single, cuneate apical cell (figs. 1 and 2), cutting off segments on four faces. CAVERS (3) reports a row of initials at the apex. In none of the preparations studied in this particular instance, however, could this report be verified. On the contrary, they seemed to show very distinctly a single apical cell, distinguished from its surrounding segments both as to its size, and also as to the size, plane, and position of its nucleus. Relative to the apical cells found in the other genera of the Marchantiales, the apical cell of *Targionia* is rather small.

The development of the air chamber is one feature which, as yet, has not been described. This proceeds along the lines reported by

Barnes and Land (4) as typical for the Marchantiales. The air chambers arise by the splitting apart of the superficial cells just

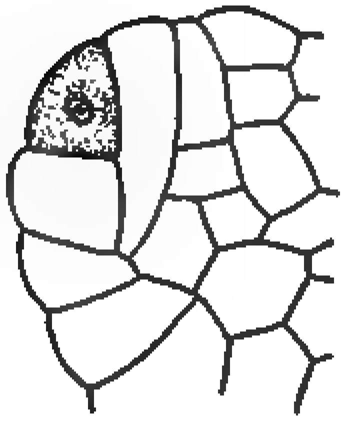


Fig. 1

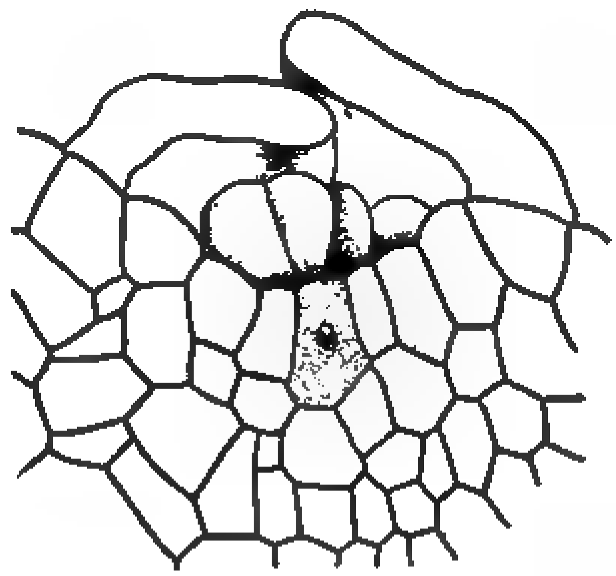


Fig. 2

Figs. 1, 2.—Fig. 1, median longitudinal section through the apical cell; fig. 2, section in horizontal plane of thallus through the apical cell.

back of the growing point (fig. 3). However, in the other Marchantiales described, this splitting originates in an angle between the epidermal and hypodermal layers of cells, and proceeds outward toward the surface; in *Targionia* the process is reversed, the cracking apart starting at the surface between two epidermal cells and proceeding inward. Subsequent divisions enlarge the space thus formed, as well as the breadth of the roof.

Early in its development the pore is closed by rapid divisions in the roof cells, and it remains closed until the chamber has almost reached maturity. The chlorophyllose filaments develop comparatively early in the history of the chamber (figs. 4–6); as soon as the chamber is 3–5 cells broad, the cells of the floor begin to project as papillae. These papillae are divided by transverse walls into filaments, which at maturity are 2–6 cells in length. They branch profusely, and in the mature chamber very

Fig. 3.—Nearly median section through growing point, showing origin of air chambers.

often are so long that they grow snugly up against the roof, thus giving the impression, in section, as though there were filaments depending from the roof of the chamber, as well as standing up from the floor. Directly beneath the pore the filaments are slightly modified, the distal cell being hyaline and containing no chloroplasts except one or two lying along the bottom wall. There is no modification in the form of

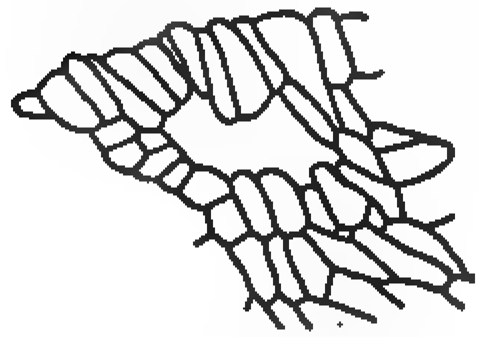


FIG. 4

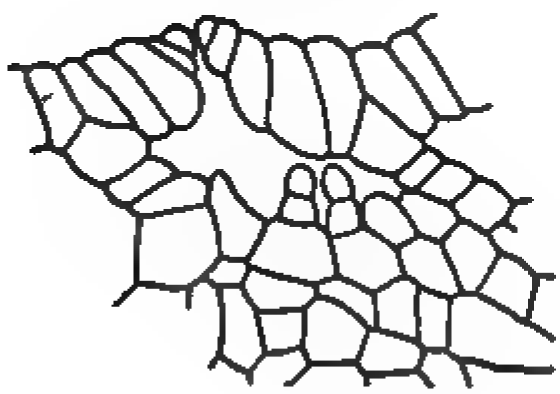


FIG. 5

FIG. 6

FIGS. 4–6.—Fig. 4, young air chamber before appearance of the chlorophyllose filaments; fig. 5, air chamber with two chlorophyllose filaments and primordium of a third; fig. 6, later stage of air chamber, showing distortion due to unequal elongation of cells of the thallus.

these hyaline cells, as there is in *Conocephalus;* they retain the same ovoid shape found in the other cells of the filament (figs. 7 and 8).

The cells surrounding the air pore are arranged in a series of concentric rings, raised crater-like a little above the dorsal surface of the thallus. The innermost ring is composed of dead cells, collapsed and highly cutinized; and is not, as stated by CAVERS, a hardened membranous ring which has been put forth by the innermost layer of cells surrounding the pore (fig. 9).

The ventral scales are placed in two rows on either side of the midrib and are of an intense dark purple or red-brown color. They are inserted on the posterior margin, and arranged on the ventral surface in a wonderfully exact and regular fashion. On the anterior margin of the scale is borne a curious little appendage (fig. 10)

which in the younger scales overlaps the growing point of the thallus, and may serve as a protective covering. The two rows of

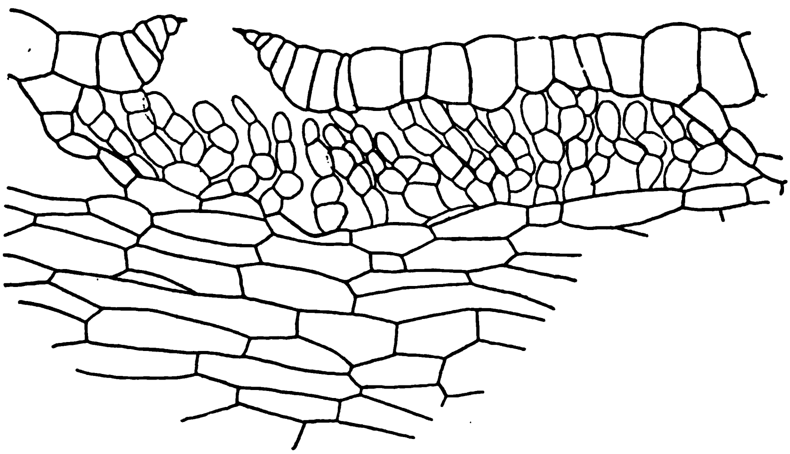


FIG. 7.—Mature air chamber in median longitudinal section

scales are separate from the first, arising from young segments close to the apical cell (CAMPBELL 2).

Both the pegged and the smooth rhizoids are present. They are extremely long, and most curiously swollen and distorted at the distal end. According to CAVERS (3) the smooth rhizoids are borne on the midrib and pass directly into the ground. The pegged rhizoids arise in great profusion in the axils of the scales and pass backward along either side of the midrib.

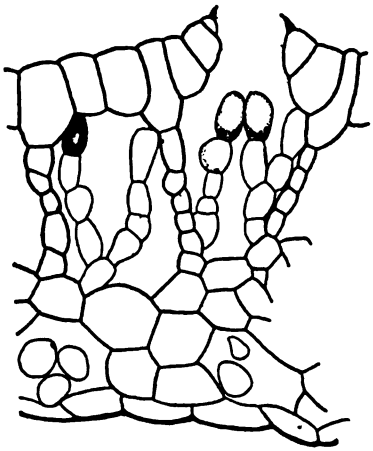


FIG. 8.—Transverse section through two air chambers, showing their extreme narrowness.

The solid, colorless tissue of the thallus is composed of elongated and, for the most part, highly vacuolate cells. These begin their elongation directly behind the growing point, and this process goes on so rapidly

that it pulls both the filaments and the vertical walls of the air chambers diagonally backward, giving the chamber a more or less distorted appearance (figs. 4–7).

A really surprising amount of differentiation is seen in the cells of the solid portion of the thallus. The commonest and most usual is a strand of stumpy cells, filled with oil globules and food granules, which passes longitudinally through the center of the thallus, and ends around the foot of the sporophyte. Besides this, there is frequently a strand composed of the ordinary elongated cells, with their walls thickened by an irregularly wound tangle of fibers, also running the entire length of the thallus.

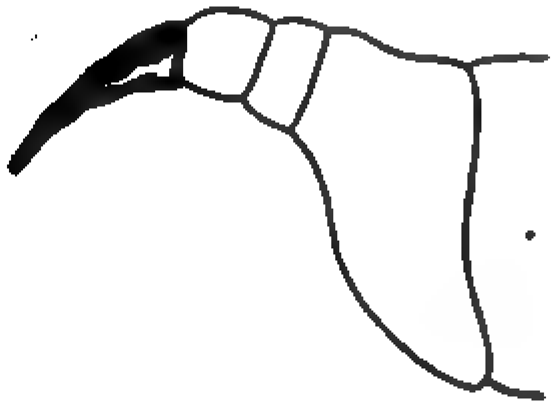


FIG. 9.—One member of the ring of collapsed cells which surround the air pore.

Vegetative reproduction.—The dichotomous branching, which is so common in the other members of the Marchantiales, is here almost entirely replaced by the occurrence of branches arising from the ventral surface. These branches have, for the most part, at maturity a stalk-like base, through the dying away of which the branches are set free as independent plants, and will then themselves multiply in the same fashion.

In their origin, these adventitious branches have absolutely nothing to do with the apical cell. This was clearly seen in several of the preparations studied, where, on a plant bearing two young branches, the older one was placed between the apical cell and the younger.

FIG. 10.—Appendage to ventral scale, which overlaps the growing point.

Archegonia.—The archegonia are borne terminal on the thallus. They follow so closely the general line of individual development for the Marchantiales, that it is not necessary to repeat it here. They arise in two rows in acropetal succession. The surface, or pad, on

which they are borne slopes forward and downward at the time the archegonia are mature. The development of this "fruiting surface" runs as follows. The archegonia, arising as they do in acropetal succession, check to a great extent the vegetative growth behind the growing point. The apical cell, however, is not immediately concerned, and continues its segmentation with practically no interruption. The natural result of this is that the apical cell is carried forward and out. Thus the archegonial surface is finally brought to lie in a sort of pit or depression in the anterior end of the thallus. On the lower and outer margin of this pit is the apical cell, which, when this stage is reached, ceases to function.

The involucre.—The development of the involucre is so closely allied to that of the archegonial surface, that it is extremely difficult to say just where the one leaves off and the other begins. It is simply the continued forward growth of the tissues immediately surrounding the shallow pit at the anterior end of the thallus, with the natural result that the opening to this pit is narrowed, and begins to close up. It is never completely closed, however, although in the earlier stages the edges of the wings are brought very close together. As the involucre matures, the outer surface, as well as the inner margin of the wings, becomes highly cutinized.

That the involucre is not, as reported by CAVERS (3), a result of the stimulus given by the act of fertilization is shown in one of the preparations, where it was complete and well developed, while the eggs of the archegonia it surrounded were still unfertilized.

Calyptra.—The calyptra is a simple and very delicate structure, soon ruptured by the growth of the sporophyte. At maturity it is 2–4 layers thick at the base.

Sporophyte body

Capsule.—The capsule is a comparatively simple affair. The wall consists of a single layer of cells, uniformly thickened with spiral and annular bands. There is no special mechanism for dehiscence. In his recent report on *Targionia*, CAVERS (3) figures and describes a rudimentary elaterophore, represented by a few spirally thickened cells depending from the distal portion of the capsule. This statement could not be verified in any of the sections

studied here, nor do either CAMPBELL (2) or LEITGEB (1) report such a condition.

True elaters are present, long, slender, fusiform, and thickened by usually two spiral bands.

The spores themselves have fairly thick walls, highly sculptured, and are produced in great numbers (fig. 11). CAVERS (3) has described the spore mother cells as lobing deeply before division, as happens in many of the Jungermanniales. All of the preparations studied here, however, show the ordinary tetrad formed from a spherical spore mother cell.

FIG. 11.—Tuberculate spore.

Seta and foot.—Both seta and foot are rather well developed. While small as compared with the size of the capsule, they are nevertheless rather massive, and well differentiated from each other. The foot is club-shaped, and bluntly pointed at the lower end (fig. 12). The surface cells project as short papillae, and are haustorial in function. These cells, as well as those of the calyptra surrounding them, show in section a very much darker stain than do the cells of the surrounding tissues. Between the calyptra and foot is interposed a fairly thick layer of mucilaginous material.

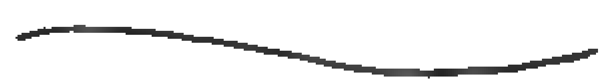


FIG. 12.—Foot and seta

Although 6–10 archegonia are produced, only one egg is fertilized. The remaining archegonia, however, persist, and are still visible after the sporophyte has matured; soon after the sporophyte has begun its development, however, their contents break down into a darkly staining mucilaginous mass.

Classification

The Marchantiaceae are at present classified according to three schemes. LEITGEB (1) gives the following:

Marchantiaceae
- *a*) Astroporae (Clevea, etc.)
- *b*) Operculatae (Plagiochasma, Fimbriaria, etc.)
- *c*) Targioniae (Targionia, Cyathodium)
- *d*) Compositae (Marchantia, Lunularia, etc.)

CAMPBELL (2, p. 67) gives the following:

Marchantieae
- *a*) Corsinieae
- *b*) Targionieae
- *c*) Marchantieae

GOEBEL has proposed still another classification. In this he transposes the Riellaceae to the *Marchantia* group, as follows:

- *a*) Corsiniaceae
- *b*) Targioniaceae
- *c*) Riellaceae
- *d*) Marchantiaceae

Without concerning ourselves with the relative merits of these schemes, it might be well to take up the one family, the Targionieae. This family at present contains but two genera, *Targionia* and *Cyathodium*, and it is with regard to the merits of placing these two genera within the same family that a question may be raised. In order the more clearly to present this question, the accompanying diagrams (fig. 13) have been prepared. In the key to these diagrams it will be seen that each generation (sporophyte and gametophyte) has been divided into four features, selected because of their bearing on a natural scheme of classification. Each of these divisions has been subdivided into five stages of as nearly equal importance as it was possible to find.

From the diagram it will be seen that the two lines coincide in but two points. The one of these is D4 and the other E4, which represent respectively the apical position of the archegonia accompanied by a checking of the growth of the thallus at this point, and the common involucre.

As for the former (D4), the character is not peculiar to this

group. In several other genera the archegonia are borne in a terminal cluster, notably *Grimaldia*, *Reboulia*, and *Clevea*. This narrows the situation down to a *single* character common to these two genera (*Targionia* and *Cyathodium*) and not found in others. This is the common involucre inclosing the terminal group of archegonia.

One glance at the diagrams will show how widely the two genera differ in all other respects save this. *Targionia* has perhaps as complex a thallus as is found in the entire group of Marchantiales;

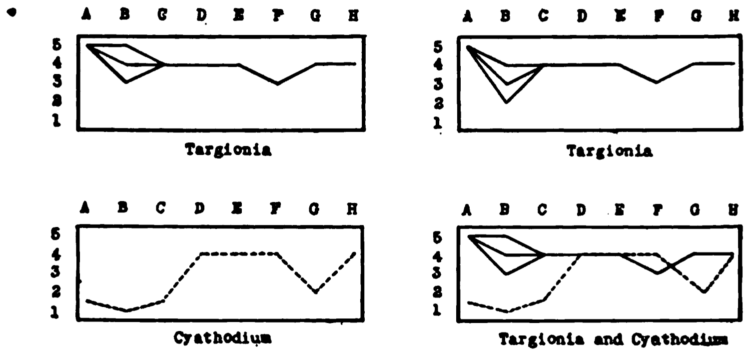


FIG. 13.—Diagrams comparing *Targionia* and *Cyathodium*

Cyathodium has perhaps the simplest, both as regards structure and the amount and character of differentiation. The thallus of *Cyathodium* consists of a simple ribbon, two layers of cells thick, the two layers slightly separated to form an air space, the air pores being simple openings in the upper layer of cells.

In *Targionia* the antheridia are borne on a special portion of a special branch; in *Cyathodium* they are scattered in clusters along the edge of the thallus. In *Targionia* the foot and seta of the sporophyte are massive and well differentiated; in *Cyathodium* both foot and seta are represented by a single filament, four cells in length.

In *Targionia* the elaters are true elaters, long pointed, and spirally banded; in *Cyathodium* the elaters, while spirally banded, are little more than dead nurse cells, short and stumpy.

In but one character is *Targionia* less advanced than *Cyathodium*, and that is in the differentiation of the capsule wall

in the mature sporophyte. In *Cyathodium*, only the cells of the upper part of the capsule are spirally thickened, so that dehiscence occurs through the formation of 6–8 fairly regular teeth.

Of course there are several difficulties in the way of such a determining scheme as this. In the first place, it is next to impossible to select characters that will be absolutely determining. In the second place, it is impossible to select groups of characters whose determining value will be equal. Again, there is the difficulty of deciding as to which of two characters is the more advanced. And finally, there is the conflict as to the relative value of sporophytic and gametophytic characters. Is a complex gametophyte with a simple sporophyte more advanced than a simple gametophyte bearing a complex sporophyte, or vice versa; to say nothing of the different gradations in combining the two.

Leaving aside, for the present, the difficulties which a practical application of this scheme presents in general, it does seem to apply in the specific case under discussion; no matter which of the two is the higher, it seems to be fairly certain that they are widely different. According to the diagrams the two genera have but the one salient feature which is common to them and to them only, a single involucre inclosing a group of terminally borne archegonia. Now it certainly does not seem as though such a character as this should be sufficient to bind two genera differing so widely in all other respects into one family.

As to where *Cyathodium* belongs, if not with the Targionieae, the Corsinieae suggest themselves readily. But such a matter as this cannot be settled definitely without a much more extended study of *Cyathodium*, as well as the family Corsinieae, with its two genera (*Corsinia* and *Funicularia*), than has been given them.

Thanks are due Professor JOHN M. COULTER and Dr. W. J. G. LAND for assistance rendered during the progress of the work.

THE UNIVERSITY OF CHICAGO

LITERATURE CITED

1. LEITGEB, H., Untersuchungen über die Lebermoose 6:131–136. 1881.
2. CAMPBELL, D. H., Mosses and ferns. 1905.
3. CAVERS, F., Contributions to the biology of the Hepaticae. Part I. *Targionia, Reboulia, Preissia, Monoclea*. 1904.
4. BARNES, C. R., and LAND, W. J. G. The origin of air chambers. BOT. GAZ. 44:197–213. 1907.

A PRECISION AUXANOMETER

W. T. Bovie

(WITH TWO FIGURES)

In the auxanometers which have been described up to the present time, a thread or string has been used to transmit the motion of the growing plant to the recording device. This construction is always faulty, because changes in humidity affect the length of the thread, and so falsify the record. The author has designed a machine which eliminates the thread and its unavoidable errors by substituting for it material which is not affected by humidity and which is very little altered by changes in temperature.

On account of the error due to the thread, it has heretofore been impracticable to use a recording device which would indicate small increments in length. On account of the great precision of the new instrument such a device is needed, and accordingly the recording mechanism has been refined until it is capable of registering an increment of a single micron.

It has hitherto been necessary, except with the auxanometer described by Frost,[1] to place the recording device in close proximity to the plant. This is cumbersome and has prevented the simultaneous recording of the growth of a number of plants. Frost's machine used a thread, but as the growth was recorded electrically, simultaneous records of the growth of several plants could be made. This valuable feature has been incorporated in the new auxanometer.

The machine consists essentially of a device which is carried upward as the plant grows. When this device has moved a certain small distance, it closes an electric circuit which operates the recording pen of a chronograph. As the connection of the plant with the circuit-closing device is made with invar, a metal with an exceedingly small coefficient of expansion with changes of temperature, the growth can be accurately measured to a very few microns, and by using a condenser in the electric circuit, as described later, the growth can be recorded to a single micron.

[1] Minnesota Botanical Studies no. 17. 1894.

The mechanism may be understood by referring to fig. 1. The plant is attached by the invar wire *a* to the small spring *b*, which pulls upward a little more than is necessary to lift the weight of the wire (the exact amount of this pull may be regulated easily by a screw not shown in the drawing). Experiment has shown that this slight pull is not enough to affect the growth of the plant.

As the spring moves upward, it comes in contact with the block *c* at the point *c'*. This closes the electric circuit, which up to this time has been open, since the spring *b* is insulated from *c* at its other point of contact. The current which now flows through the line energizes the coil *d*, which draws the escapement lever upward. The block *c* is carried on the screw *f*, which is connected by a train of wheels at *f'* to a clock spring, which tends to turn the screw in such a manner as to raise the block *c* upward. The screw is prevented from turning by the escapement lever *e*, but when the escapement lever is drawn up by the magnet *d*, it allows the screw to turn a given part of a revolution. The block *c* is therefore raised a certain distance and the circuit opened. The plant must now grow exactly this distance before the circuit is closed again.

The upward movement of the block *c* is determined by the pitch of the thread of the screw *f* and the amount it turns. By changing the number of teeth in the escapement wheel at the top of the screw *f*, the amount it turns at each contact can be controlled. There are 20 teeth in the escapement wheel, and so the screw can be made to turn 1/20 of a revolution, or if part of the teeth are removed, it will turn more, up to a complete revolution. If the pitch of the screw is 0.5 mm., each record represents 25μ.

It may be noted, in passing, that the micrometer screw has become the standard device for measuring small distances. It is not the purpose of this account to give the mechanical specifications of the apparatus; there are many ways in which the various details can be constructed. It may be said, however, that the screw should be straight and accurate. (The screw from a phonograph, with its nut, is an excellent and inexpensive micrometer.) It should turn easily and run true in its bearings, and the nut in the block *c* should be so constructed as not to bind. In this machine use is made of a split nut which is tightened by a conical cap into which it fits.

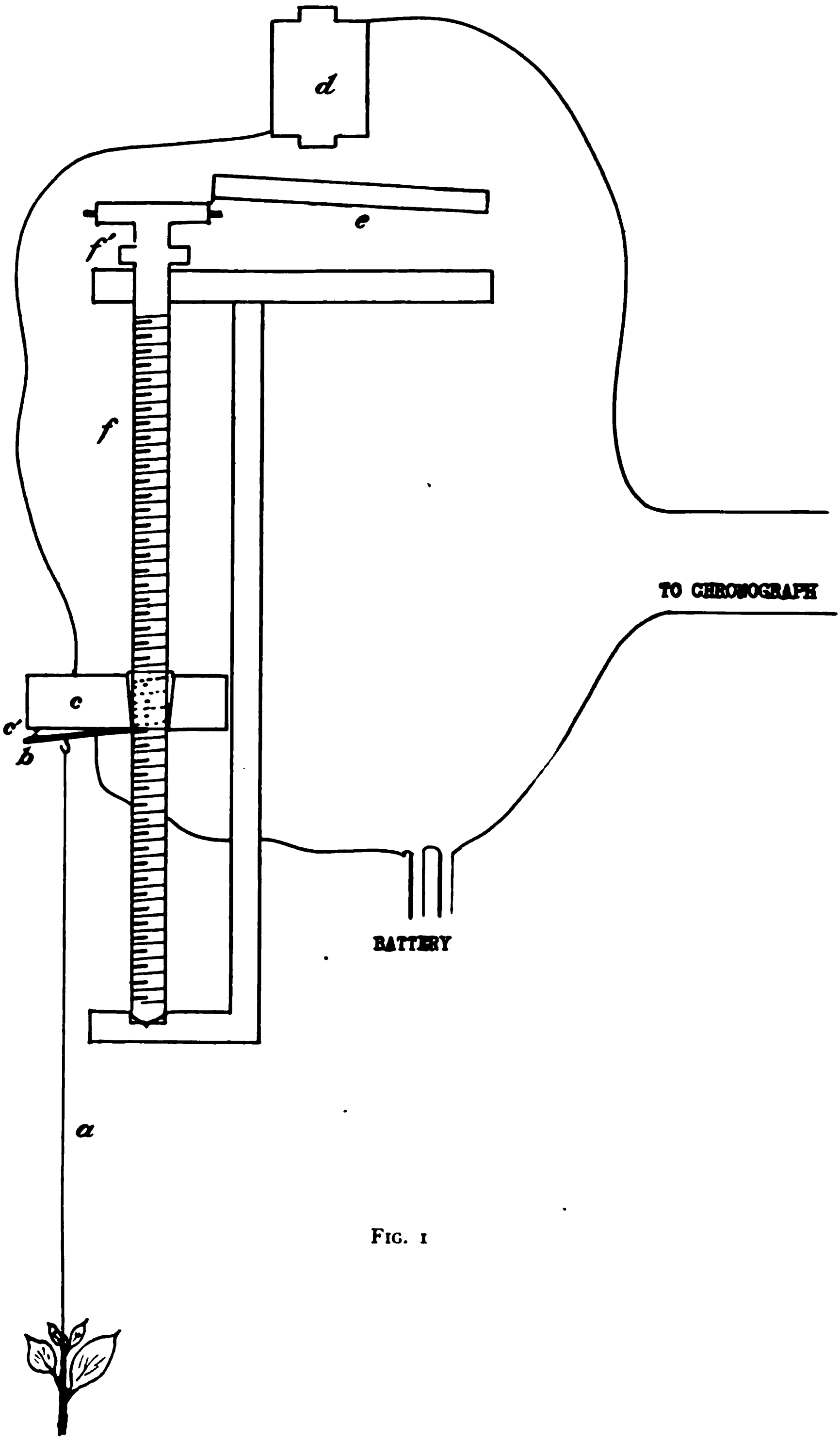


FIG. 1

The escapement should be such that one (and only one) tooth of the escapement wheel can pass at one closing of the circuit. This becomes important when the screw has to make a complete revolution for each record.

The chronograph was constructed especially for this apparatus. The drum turns once in six hours, and is of such a diameter that 1 mm. on the drum corresponds to one minute in time. The drum is long enough to receive the records from six auxanometers at one time, and holds one week's record. The pens are stationary, the drum turning under them and moving forward in the line of its own axis, so that each pen traces a spiral on the record sheet. At each closing of the circuit the pen makes a check in the line traced. When the record is removed for reading, we have a series of parallel lines, each representing six hours of time. By counting the number of checks in a given length of time, or by measuring the distance between the checks, the rate of growth can be determined.

By means of a small switchboard, an electric bell or an electric light can be included in the circuit, so that each time an increment of growth is recorded the light flashes and the bell rings. This is used only for lecture experiments. A tungsten lamp should be employed, as the length of contact is so short that an Edison lamp does not have time to become luminous.

An elongating hyacinth peduncle, which had been in the damp greenhouse and was removed to the dry air of the lecture-room, gave a record a little oftener than once a minute. Had the plant been left in the greenhouse and only the chronograph taken to the lecture-room, the contacts would have been more frequent. A young sunflower seedling gave a record every 18 seconds. Such records are too frequent for experiments of long duration, as there are too many checks to count. When working with plants growing at this rate, some of the teeth in the escapement wheel should be removed.

The principle of having the plant automatically close and open an electric circuit during growth permits the increase in length to be measured to almost any degree of accuracy. The only difficulty is a tendency to arcing across the spark gap between the spring *b* and the block *c*. There are two ways of preventing this: the wire

a may be attached near the fixed end of the spring *b*, thus making the gap longer than the distance recorded, or a condenser (such as is used in a telephone for instance) may be placed around the gap. The latter method will also tend to prevent burning of the terminals. Terminals of platinum and gold give the best results. Even with these precautions there will be a limit to the accuracy of a

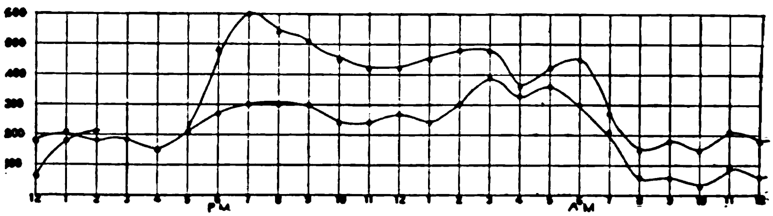


FIG. 2.—Curve of rate of growth of the hypocotyl of a four-o'clock seedling; abscissas indicate time, ordinates growth per hour in microns; total time recorded, 46 hours; total growth recorded, 1.75 cm.

Time	1	2	3	4	5	6	7	8	9	10	11	12
Checks per hour	..	..	..	5	7	16	20	18	17	15	14	14
	15	16	16	12	14	15	9	5	6	5	7	6
	7	6	6	5	7	9	10	10	10	8	8	9
	8	10	13	11	12	10	7	2	2	1	3	2
	6	7	..	..	..	..	..	..	..	..	..	..

single record, for the two metal surfaces will not always give electrical contact at the same place. But as any experiment includes a great number of records, these slight errors will average up so that the results will be absolutely accurate.

A record is given in fig. 2 of a four-o'clock seedling for the first 46 hours after it appeared above the ground. The making of this record put the machine to an extreme test, as these seedlings are very delicate. It will be noted that the curve is very even, and that it passes very close to the points from which it is plotted. The relation of the rate of growth to light is clearly shown. The records were made in January, when the laboratory darkened early. The temperature of the laboratory falls considerably at night, getting coldest at 4 o'clock in the morning, at which time the day fireman starts up the fires. It will be noted that on both nights the rate of growth changes sharply at this point. The first inter-

node did not elongate as much on the second day as it did on the first, hence the curve for this day is everywhere below the first one. Very interesting curves can be produced when several plants are compared, or when the increments of the various internodes of the same plant are recorded simultaneously.

The writer is now working in cooperation with the L. E. Knott Apparatus Company on a new model, which involves a different mechanism for opening the circuit. This machine will be smaller, and it is hoped that it can be put on the market at a very low cost.

Harvard University
Laboratory of Plant Physiology

BRIEFER ARTICLES

SOME PLANTS OF WESTERN AMERICA

Several collections of plants from western America have recently been submitted to the writer for identification, and among them a number have been found of especial interest, either because of their geographical distribution or because they represent species which apparently have not been described hitherto; these may be recorded and diagnosed as follows:

ROMANZOFFIA UNALASCHCENSIS Cham. in Nees. Hor. Phys. Berol. 72, *t. 14*, 1820.—Specimens collected on the northeast aspect of vertical cliffs, three feet above high sea-level, Albert Head, British Columbia, 6 June, 1907, *Dr. C. F. Newcombe*, no. 324 (hb. Field Museum, cat. no. 250181) correspond in all essential details with a part of the original material in the Gray Herbarium on which the above species was founded. This station extends the range of the species considerably south from previously recorded localities.

Castilleja arachnoidea, n. sp.—Herbacea perennis; caulibus caespitosis erectis 2–3 dm. altis in partibus inferioribus crispo-hirsutis, superioribus arachnoideo-tomentosis; foliis 1.5–4 cm. longis linearibus vel anguste lanceolatis et integris plerumque trifido, laciniis linearibus acutis patentibus, lobo intermedio majore et saepe trifidis; inflorescentiis terminalibus dense spicatis 10–13 cm. longis; bracteis plerumque trifidis, lobo intermedio integro et obtuso vel apice trilobulato; calyce 15–17 mm. longo extrinsecus piloso antice et postice subaequaliter fisso; lobis lateralibus profunde partitis, laciniis lineare-lanceolatis acutis 7–10 mm. longis; corolla 17–20 mm. longa extrinsecus pubescente flava vel lobis in sicco paululo rubellis; galea erecta circiter quadruplo brevior quam tubus; labium trilobum 5–6 mm. longum; capsula oblonga 10–12 mm. longa acuminata acuta glabra.

On mountain summits near Marble Mountain, Siskiyou County, Cal., altitude 2000 m., 6 August, 1908, *Geo. D. Butler*, no. 422 (hb. Field Museum, cat. no. 276765).

In general habit this species resembles *C. Lemmoni* Gray, *C. pilosa* (Gray) Rydb., *C. pratensis* Heller, and *C. oresbia* Greenm.; it also approaches *C. ambigua* Jones, but differs in having a shorter corolla and in the nature of the pubescence. The arachnoid tomentum, long dense spikes, and conspicuous long lower lip of the corolla are the striking characters of the species.

Castilleja schizotricha, n. sp.—Herbacea perennis tota planta substellato-albido-tomentosa; caulibus caespitosis simplicibus erectis vel ascendentibus 1–1.5 dm. altis; foliis lineari-lanceolatis et integris vel trifidis 1–1.5 cm. longis 2–5 mm. latis, laciniis linearibus acutis patentibus; inflorescentiis purpureis terminalibus dense spicatis 5–9 cm. longis; bracteis saepissime trifidis circiter 1.5 cm. longis, lobis lateralibus linearibus acutiusculis, lobo intermedio lanceolato-oblongo acuto; calyce 15–17 mm. longo extrinsecus substellato-albido-tomentoso et stipitato-glanduloso antice et postice aequaliter fisso, laciniis lateralibus profunde partitis lineari-attenuatis acutis dense substellato-tomentosis; corolla purpurea 15–17 mm. longa, galea erecta 4 mm. longa circiter quater brevior quam tubus, labio circiter 4 mm. longo basi triplicato, labii lobis lineari-oblongis 2 mm. longis obtusis; capsula oblonga 8–10 mm. longa brevi-acuminata acuta glabra.

On summit of mountain, near Wooly Creek, Siskiyou County, Cal., altitude 1830 m., 5 August, 1908, *Geo. D. Butler*, no. 423 (hb. Field Museum, cat. no. 276766).

The species here described is apparently most nearly related to *C. brachyantha* Rydb., *C. Covilleana* Hend., and *C. pilifera* Nels. From all these it is readily separated by the branched hairs and the characters of the calyx.

Senecio Suksdorfii, nom. nov.—*S. Adamsi* Howell, Fl. N.W. America 1:379, 1903, not *S. Adamsii* Cheesm. Trans. N.Z. Inst. **28**:536, 1896. Mr. HOWELL's specific name for this plant coincides so closely with the name given by Mr. CHEESEMAN to a New Zealand species of this genus that it seems desirable to give our American plant a new specific name; and the writer takes pleasure in associating therewith the name of Mr. W. N. SUKSDORF, who has done so much to further our knowledge of the plants of Washington.

Hereto are referred the following: on rocky ridges, Mt. Paddo (Adams), Washington, altitude about 2155 m., 9 August, 1882, *W. N. Suksdorf* (hb. Gray, hb. Geol. Surv. Canada, and hb. Field Museum); east of Mt. Adams, August, 1892, *L. F. Henderson*, no. 2309 (hb. Gray); Yakima region, 1883, *T. S. Brandegee*, no. 915 (hb. Gray); Indian Henry Park, September, 1909, *J. B. Tarleton*, no 62 (hb. Field Museum); at the base of granite cliffs, source of the Imnaha, Wallowa Mts., Oregon, altitude 2690 m., 14 August, 1906, *Wm. C. Cusick*, no. 3131 (hb. Field Museum); on Mt. Rose, Nevada, altitude 2970 m., 29 July, 1909, *A. A. Heller*, no. 9896 (hb. Field Museum).

Senecio (§ AMPLECTENTES) **Websteri,** n. sp.—Herbaceus perennis; caulibus erectis vel ascendentibus 1.5–2 dm. altis parce floccoso-tomentulosis; foliis inferioribus petiolatis subovatis vel oblongo-obovatis 8–12 cm. longis 1.5–4.5 cm. latis acutis denticulatis vel sinuato-dentatis

basi decurrentibus membranaceis utrinque arachnoideo-tomentulosis plus minusve glabratis, petiolis alatis, foliis superioribus sessilibus lanceolatis irregulariter dentatis; pedunculis elongatis usque ad 8 cm. longis unicapitatis; capitulis 1.8–2 cm. altis multifloris radiatis subnutantibus; involucris campanulatis calyculatis; squamis involucri lineari-lanceolatis 13–15 mm. longis apice acutis penicillatis extrinsecus arachnoideo-tomentulosis; floribus femineis 12–15, ligulis lanceolato-oblongis 12–15 mm. longis 3–4 mm. latis flavis; floribus disci numerosis, corollis ca. 8.5 mm. longis; pappi setis albidis subaequantibus; achaeniis glabris.

On talus slopes of Mt. Angeles, Clallam County, Washington, altitude about 2000 m., 2 September, 1909, *E. B. Webster*, no. 109 (hb. Field Museum cat. no. 251971).

In habit *S. Websteri* is similar to *S. seridophyllus* Greene which, however, is glabrous throughout and has smaller heads and shorter rays. In foliar characters *S. Websteri* resembles *S. Elmeri* Piper, but differs in having much larger and solitary heads. Mr. E. B. Webster of Port Angeles, by whom the specimens were collected, in commenting on the plant, states: "There are possibly a hundred plants in all, a few growing at the northern side of the base of one of the pinnacles, the remainder being scattered along the narrow rocky talus for possibly 1000 ft.; on the slope at the base of the pinnacle *Arnica cordifolia* Hook. and *Heuchera racemosa* Wats., both rare on Mt. Angeles, were associated with the *Senecio*, and somewhat lower down *Hedysarum occidentale* Greene and *Arabis Lyallii* Wats. were growing along with it."—J. M. Greenman, *Chicago*.

SOIL MOISTURE IN THE COTTONWOOD DUNE ASSOCIATION OF LAKE MICHIGAN

(WITH ONE FIGURE)

The following data regarding the range of soil moisture in the cottonwood dune association upon the shores of Lake Michigan seem to be of sufficient interest to warrant their publication in advance of the results of more extensive studies of the same sort now in progress. The work of Cowles[1] upon its general ecological relations and that of the writer[2] upon the evaporating power of the air have shown this to be an open association of a single tree species, together with a scanty undergrowth

[1] Cowles, H. C., The ecological relations of the vegetation of the sand dunes of Lake Michigan. Bot. Gaz. 27:95–391. 1899.

[2] Fuller, G. D., Evaporation and plant succession. Bot. Gaz. 52:193–208. 1911.

of shrubs and grasses, developing upon more or less rapidly moving dunes, possessing a very high rate of evaporation, exhibiting many strongly xerophytic characters, and almost entirely dependent upon vegetative reproduction for its maintenance. The almost complete absence of herbaceous undergrowth and the expanse of bare sand give it a desert-like aspect, but below the superficial layer of dry sand an abundant and unfailing water supply has been found.

From the beginning of May to the end of October 1911 duplicate samples of about 125 grams of soil were taken weekly at depths of 7.5 cm. and 25 cm., the soil dried at 104° C., and the ratio of water to the dry weight of soil found to range from 2 to 8 per cent, an apparently very inadequate amount.

Until recently no satisfactory means of relating such soil moisture determinations to plant growth have been available but the "wilting coefficient" of BRIGGS and SHANTZ[3] now indicates the limit of soil water content above which growth must occur, although plants will live and continue to draw water from the soil much below this limit. Further, the same workers have shown that many plants differ very little in their wilting coefficients from the standard Kubanka wheat. As under ordinary conditions a water supply very little above that at which wilting occurs is sufficient for some growth, the difference between the soil moisture actually present at any time and the wilting coefficient of the soil represents approximately the amount of water available for purposes of growth, and this, in the absence of a better term, may be referred to as "growth water."

Following the methods of BRIGGS and SHANTZ (*loc. cit*), the wilting coefficient of the dune soil was found to be 0.75 per cent at both depths, the absence of humus accounting for this similarity. Graphically representing this wilting coefficient and plotting the soil moisture determinations as graphs having the weekly intervals as abscissae and the percentage of water present in the soil as ordinates (fig. 1), it will be seen that the moisture present in the soil of the cottonwood dune is at all times more than double the wilting coefficient, or in other words there is always present at least twice the amount of water necessary for the growth of such a plant as wheat. Throughout the most arid portion of the season, namely the ten weeks beginning with the first of July, the surplus or growth water averages 2.2 per cent, showing that,

[3] BRIGGS, L. J., and SHANTZ, H. L., The wilting coefficient for different plants and its indirect determination. U.S. Dept. Agric., Bur. Pl. Ind. Bull. 230, 1912; also BOT. GAZ. 53:20–37, 229–235. 1912.

considered upon the basis of its soil moisture, the association is decidedly mesophytic. The causes of the xerophytic character of the vegetation must be sought in the high evaporating power of the air and in the instability of the substratum. These factors, however, doubtless react upon the surface of the soil and tend to conserve the soil water by constantly maintaining a dry surface mulch. The constant presence of a sufficient amount of moisture perhaps will help to explain the readiness

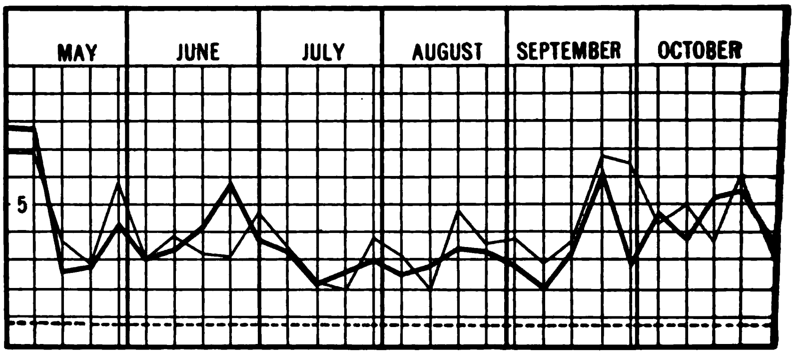


FIG. 1.—Graphs showing the range of soil moisture in the cottonwood dune; the heavy line at 7.5 cm. and the light line at 25 cm. depth; wilting coefficient represented by a broken line.

with which vegetative reproduction occurs within the association, while the shifting sand and high rate of evaporation may account for the almost entire absence of seedlings of any sort.

From these scanty data it would seem that determinations of soil moisture, related to plant growth through the wilting coefficients of the soil, will afford an efficient means of making quantitative studies of the water supplies of the subterranean parts of plant associations, and, as in the present instance, enable students of ecology to analyze more closely the effects of the various factors influencing the production of any particular plant association.—GEO. D. FULLER, *The University of Chicago.*

CURRENT LITERATURE

BOOK REVIEWS

Texts for secondary schools

The authors of ***Applied biology***[1] do not wish to indicate by the title any unusual predominance of economic material. Their book is a text of general

The book by PEABODY and HUNT[3] is principally interesting as illustrating a very distinct recent tendency in elementary botanical instruction. It will be recalled that not long since our elementary texts emphasized morphology and anatomy. Of late the new books have been giving more and more space to the physiology and ecology of seed plants. The book under review carries this to the extreme by relegating the morphology to a final "optional" chapter. Such an extreme position will scarcely be accepted generally, but the tendency in that direction is unmistakable.

The tendency toward the abbreviation of the morphological part of the work is evident also in *Experimental botany*.[4] The last chapter in the book takes up the "cryptogams." This book is a laboratory manual rather than a textbook, though there is a small amount of descriptive text. Its unique feature is in the experimental attitude which is maintained throughout. The author feels that botany should be taught experimentally in the same sense that physics or chemistry is so taught; the selection of physiological materials follows naturally. The laboratory directions appear to be workable. A large number of the experiments are new to elementary texts. The new point of view and the new experiments make it a stimulating book for teachers.

The laboratory manual by FRYE and RIGG[5] is intended to meet the needs of teachers on the Pacific slope. The species suggested for laboratory work are selected with reference to the western flora. The directions for work are well written, and it is in every way an excellent little book. While it is written with western conditions in mind, and must be particularly welcome in that part of the country, it would be quite usable in the East as well.—W. L. EIKENBERRY.

MINOR NOTICES

Flora of Porto Rico.—The publication of the fourth fascicle of Vol. IV of URBAN'S *Symbolae Antillanae*,[6] which includes the sympetalous groups from the genus *Tamonea* of the Verbenaceae to the end of the Compositae, under the subsidiary title of *Flora portoricensis*, brings to a close a consideration of one of the most interesting of our insular floras. New species are described in *Priva*, *Dicliptera*, and *Psychotria*. The taxonomic part is followed by a *Nachwort*, in which the author sets forth the purpose of the work and reviews

[3] PEABODY, J. E., and HUNT, A. E., Elementary plant biology. 8vo. pp. xvi+207. *figs. 91*. New York: Macmillan. 1912.

[4] PAYNE, F. O., Manual of experimental botany. 8vo. pp. *272*. *figs. 117*. New York, Cincinnati, Chicago: American Book Co. 1912.

[5] FRYE, T. C., and RIGG, G. B., Laboratory exercises in elementary botany. 8vo. pp. xxii+139. Boston: Ginn & Co. 1911.

[6] URBAN, IGNATIUS, Symbolae Antillanae seu fundamenta florae Indiae Occidentalis, Vol. IV, fasc. 4. pp. 529–771. Flora portoricensis. Leipzig: Fratres Borntraeger. 1911.

briefly the circumstances under which the study was begun, developed, and brought to completion. A brief but interesting chapter is devoted to a history of botanical exploration in Porto Rico from the earliest collections made in 1785–1786 to the recent expeditions by different members of the staff of the New York Botanical Garden. A careful tabulation shows that 2056 species, representing 167 families of Pteridophytes and Phanerogams, are known from the island at the present time. Of this number 271 species, or 13.13 per cent, are peculiar to the island. The families best represented in numbers of species are: Polypodiaceae (182), Leguminosae (136), Gramineae (122), Compositae (90), Orchidaceae (86), and Cyperaceae (85). From a detailed analysis of the species recorded, Professor URBAN concludes that the flora of Porto Rico is most closely allied to that of South America. A very complete index to the Latin and vernacular names terminates the volume. The work forms a reliable and authoritative basis for future investigations on the flora of this interesting and economically important insular territory.—J. M. GREENMAN.

Flora of Formosa.—Since the publication of the *Enumeratio plantarum Formosanarum* in 1906 and the *Flora montana Formosae* in 1908, investigations on the flora of the island of Formosa have been pushed forward with astonishing vigor, which is amply attested to by the appearance of another volume entitled *Materials for a flora of Formosa.*[7] The author in the present volume has attempted to enumerate all species recorded from the island since the publication of the works mentioned above. Flowering plants, ferns, and fern-allies only are included, and these are chiefly from the mountainous regions of the island. Over 700 species are listed, representing 343 genera and 109 families, thus making the total number of species known up to the present time 2660, representing 836 genera and 156 families. The work of identification of the plants on which this contribution to knowledge is based has been carried on at Tokyo, Kew, Paris, Berlin, and St. Petersburg, and over 300 species and several varieties are characterized as new to science. The location of the island of Formosa is such that its flora is composed of elements common to Japan, China, India, and the Malayan region. The large number of novelties recorded is suggestive of a very rich and varied flora, and indicates, moreover, that Formosa is still a fruitful field for further taxonomic investigation.—J. M. GREENMAN.

NOTES FOR STUDENTS

Biology of rusts.—MÜHLETHALER, who has made a large number of cultural experiments with the crown rusts of grasses in Switzerland, has given a complete account of his investigations, a part of the results of which have already been published in a preliminary account.[8] Since DEBARY's demon-

[7] HAYATA, B., Materials for a flora of Formosa. Jour. Sci. Coll. Tokyo 30:1–471. 1911.

[8] Rev. BOT. GAZ. 51:157. 1911.

stration of the connection between the crown rusts of grasses and the aecidia occurring on species of *Rhamnus*, these rusts have been more especially investigated by ERIKSSON and by KLEBAHN, with the result that two species have been differentiated: *Puccinia coronata* (Corda) Kleb. with aecidia chiefly on *Rhamnus Frangula;* and *P. coronifera* Kleb. with aecidia chiefly on *R. cathartica*. These comprise several form-species whose teleutospore generation in each case is confined to a small group of grasses. To these collective species MÜHLETHALER[9] has added a third, described as *P. alpinae-coronata* with aecidia on *Rhamnus alpina* and *R. pumila*.

The cultural work, which covers an unusually large number of infection experiments, emphasizes more strongly the facts already suggested in the work of KLEBAHN and of ERIKSSON, that the crown rusts are not so strictly limited, in their specialization, to certain hosts as some of the earlier experiments would seem to indicate, and that some of the form-species formerly established should not be kept separate. Thus, for example, the form occurring on the members of the genus *Lolium* can be transferred to members of the genus *Festuca*, showing that a sharp separation of f.sp. *Lolii* and f.sp. *Festucae* is impossible. There is also evidence to show that the degree of specialization of different forms is not the same in different regions, a fact which JACZEWSKI[10] has already pointed out in his studies on Russian grain rusts. Unfortunately, the present experiments were not continued long enough to bring out all the interrelationships of the different form-species. The cultures reported comprised (1) infection of grasses either directly by aecidiospores, or indirectly by uredospores derived from the aecidiospore infection; and (2) infection of members of the genus *Rhamnus* by teleutospores from these grasses. The aecidial material was mostly gathered in its native habitat, so that there could be no assurance of its purity, and the experiments were not continued long enough to isolate with certainty the different form-species whose aecidia occur on the same species of *Rhamnus*. For these reasons, no attempt is made in this review to distinguish between the different form-species. For experimental evidence bearing on this point the original paper must be consulted.

Aecidiospores from *Rhamnus Frangula*, or the uredospores derived from these, infected *Phalaris arundinacea*, *Calamagrostis arundinacea*, *Glyceria fluitans*, and *Anthoxanthum ordoratum* (doubtful). Teleutospores (sporidia) from *Phalaris arundinacea* infected *Rhamnus Frangula*, *R. Purshiana*, *R. californica*, *E. imeretina* (spermagonia), and *R. alaternus* (spermagonia).

Aecidiospores from *Rhamnus cathartica*, or the resulting uredospores, infected, in one series, *Lolium perenne*, *L. rigidum*, *L. italcum*, *L. temulentum*, *L. remotum* var. *aristatum*, *Festuca elatior*, *F. arundinacea*, *Phleum pratense* (poorly), and *Dactylis glomerata* (poorly). The teleutospores from *Lolium*

[9] MÜHLETHALER, F., Infektionsversuche mit *Rhamnus* befallenden Kronenrosten. Centralbl. Bakt. II. **30**:386–419. 1911.

[10] Rev. BOT. GAZ. **51**:75. 1911.

perenne and *L. rigidum* infected *Rhamnus cathartica*, *R. utilis*, *R. dahurica*, *R. saxatilis*, and *R. imeretina*. In another series the aecidiospores from *R. cathartica*, or the resulting uredospores, infected *Bromus erectus* and its var. *condensatus*; *B. sterilis*, *B. inermis*, *B. tectorum*, *B. secalinus*, *B. commutatus*, *Festuca varia*, *F. arundinacea*, *F. alpina*, *F. gigantea*, *F. violacea*, *F. rubra* (poorly), and *Lolium perenne* (1 sorus). The teleutospores from *Bromus erectus* (collected in nature) infected *Rhamnus cathartica*, *R. utilis*, *R. saxatilis*, and *R. dahurica;* and the teleutospores from the foregoing aecidial infection on *Festuca arundinacea* infected *R. cathartica*, *R. utilis*, *R. dahurica*, *R. saxatilis*, *R. imeretina*, and *R. alaternus*.

Aecidiospores from *Rhamnus pumila* infected *Calamagrostis varia*, and the teleutospores from this grass infected *R. pumila*, *R. alpina*, *R. Purshiana*, *R. californica*, *R. imeretina*, and *R. Billardi* (spermagonia).

The following cultural experiments with rusts are reported by MAYOR[11] in Neufchatel, Switzerland. The form of *Puccinia* on *Carex digitata* infected *Ribes alpinum* and *R. Grossularia*, and that on *C. glauca* infected *R. alpinum*, the reverse sowing being also made in the latter case. The forms of *Puccinia* on these two species of *Carex*, therefore, belong to the Ribesii-Caricis group of KLEBAHN, but the data are insufficient for determining if they belong to any of the five species into which KLEBAHN has divided that group. To the hosts of *Puccinia longissima* whose alternate generations occur on species of *Koeleria* and *Sedum* the author adds *K. valesiaca*, teleutospores from that host having infected *Sedum reflexum*. A form of *Puccinia* from *Carex muricata* infected *Crepis biennis* but not *Taraxacum*. It seems, therefore, that this rust is distinct from *P. sylvatica*. *Puccinia Actaeae-Elymi* is described as a new form with teleutospores on *Elymus europaeus* and aecidia on *Actaea spicata*. This form does not infect *Triticum caninum* and therefore is distinct from *P. Actaeae-Agropyri* Fischer, which has teleutospores on that host and aecidia on *Actaea spicata*.

A series of infection experiments made by DIETEL[12] with *Hyalospora Polypodii* on *Cystopteris fragilis* is the first attempt at cultural experiments with a fern rust. *Hyalospora* produces thin-walled and thick-walled uredospores, and apparently only rarely teleutospores. Sowings were made on *Cystopteris* both with fresh uredospores and with uredospores that had been left in the open during the winter. In both cases infection occurred easily. In the newly formed sori thin-walled uredospores were first produced, and these were followed later by the thick-walled form. Teleutospores were not observed. The author believes, as a result of these experiments and the rare occurrence of the

[11] MAYOR, EUG., Récherches expérimentales sur quelques Urédinées hétéroiques. Ann. Mycol. 9:341–362. *figs. 3.* 1911.

[12] DIETEL, P., Über einige Kulturversuche mit *Hyalospora Polypodii* (Pers.). Magn. Ann. Mycol. 9:530–533. 1911.

teleutospores, that this rust normally maintains itself by means of the hibernating uredospores.

In a paper which is the eleventh of a series of reports on his well-known cultural work with plant rusts, carried on since 1899, ARTHUR gives the results of the cultures of 1910.[13] The work of that year was under the immediate charge of Miss IRMA A. UHDE. Sowings of spores of 21 species of rusts on a large number of possible aecidial hosts gave no infections. Successful cultures with 34 species supplemented or confirmed the results previously obtained either by the author or by other American and European investigators. The following six forms have been connected with their antithetic generation for the first time: *Puccinia Crandalii* Pam. & Hume on *Festuca confinis* Vasey and *Symphoricarpus racemosus* Michx.; *P. quadriporula* Arth. on *Carex Goodenovii* J. Gay and *Aster paniculatus* Lam.; *Puccinia Lithospermi* E. & K. on *Evolvulus pilosus* Nutt., autoecious; *Uromyces acuminatus* Arth. on *Spartina Michauxiana* A. S. Hitch. and *Polemonium reptans* L.; *Coleosporium Vernoniae* B. & C. on *Vernonia crinita* Raf. and *Pinus Taeda* L. (aecidiospores sown on *Vernonia*); and *Melampsora Albertensis* Arth. on *Populus tremuloides* Michx. and *Pseudotsuga mucronata* (Raf.) Sudw.

The host relations of some of the *Peridermium* rusts in Nova Scotia have been studied by FRASER,[14] who, in addition to a number of field observations, reports cultures with the following forms. Teleutospores of *Melampsoropsis Cassandrae* (Peck and Clinton) Arth. from *Chamaedaphne calyculata* (L.) Moench sown on *Picea rubra* (Du Roi) Dietr. produced *Peridermium consimile* Arth. & Kern. Teleutospores of *M. abietina* (Alb. & Schw.) Arth. from *Sedum groenlandicum* Oeder also sown on *Picea rubra* produced *Peridermium abietinum* (Alb. & Schw.) Thüm. *M. ledicola* (Peck) Arth. from *Ledum* produced *Peridermium decolorans* Peck on *Picea canadensis*. One form, *Uromyces Peckiananus* Farlow on *Distichlis spicata* (L.) Greene, not belonging to the *Peridermium* rusts, produced aecidia on *Atriplex patula* var. *hastata* (L.) Gray and *Chenopodium album* L.

FISCHER'S[15] review of the work done on the biology of rusts in 1910 will be of interest to students of this group.—H. HASSELBRING.

Cytology of the Basidiomycetes.—Among the many papers which have lately appeared on the cytology of the higher fungi, three are of more than usual interest. FRIES,[16] in a brief paper on *Nidularia*, finds the mycelium and young basidia binucleated, the nuclei having the chromatin in two conspicuous masses. The nuclei increase in size with the growth of the basidium, gradually

---

[13] ARTHUR, J. C., Cultures of Uredineae in 1910. Mycologia 4:7–33. 1912.

[14] FRASER, W. P., Cultures of some heteroecious rusts. Mycologia 3:67–74. 1911.

[15] FISCHER, ED., Die Publicationen über die Biologie der Uredineen in Jahre 1910. Zeitschr. Bot. 3:620–623. 1911.

[16] FRIES, ROB. E., Über die cytologischen Verhältnisse bei der Sporenbildung von *Nidularia*. Zeitschr. Bot. 3:145. 1911.

approach, and fuse as they near the apex. The fusion nucleus increases greatly in size and forces the vacuoles, which had hitherto occupied a position between the nucleus and the end of the basidium, toward the periphery. Stages in this process are hard to follow because of the rapidity of development, but finally the single nucleole comes to lie in a tangle of chromatin in an otherwise clear nucleus. This seeming synapsis leads to a spireme stage which must be of rather long duration because of the many found. Parallel fibers are noted which become more conspicuous as the fibers shorten and segment, giving a characteristic diakinesis. At this stage the nuclear membrane has disappeared, but there is as yet no trace of spindle fibers. In the lower portion of the basidium there appears at this time a network of fibers, which finally partly surround the nuclear material, but which, however, seem to have nothing to do with the formation of the spindle. The long narrow spindle, seemingly of only three fibers, suddenly makes its appearance. Conspicuous centers are noted, but there is no trace of any radiations from either center. No definite equatorial plate was formed, but during anaphase 6–8 chromosomes were noted, one-half of which passed to either pole. No resting stage follows the division, the secondary spindles appearing at once, shorter, broader, and having two chromosomes at each pole when the process is completed. Four rather large nuclei are formed and gradually migrate toward the base of the basidium. Sterigmata develop and the nuclei become beak-shaped and pass into the developing spore and again divide. In some instances it was found that the nuclei begin to divide while still in the basidium, the process being completed when the spore is reached.

KNIEP[17] finds in the mycelium from a single spore only one nucleus in each cell, and this condition persists even in cultures a year old. He finds in young cultures (3–4 weeks) that basidia are produced without the formation of a normal fruit body. These basidia may or may not be developed from terminal cells, and each contains a single nucleus. This is somewhat larger than the nuclei of the mycelium, but according to KNIEP is never due to a fusion. Each contains a conspicuous nucleole and a dense tangle of chromatic material connected to the nuclear membrane by numerous strands. The nucleus increases in size with the growth of the basidium, the nuclear material becomes granulated, at times parallel threadlike portions are noted, the nucleole decreases in size, and the dark-staining chromatic material becomes very much contracted. At this stage conspicuous double threads are observed. This stage, which very much resembles synapsis, precedes the formation of a spireme, during which the nucleus migrates to the apex of the basidium, where follows a rapid contraction of chromatic material accompanied by the disappearance of the nuclear membrane. KNIEP was able to count at this stage four masses of chromatin from which radiations extended into the cytoplasm, giving very

[17] KNIEP, HANS, Ueber das Auftreten von Basidien im einkernigen Mycel von *Armillaria mellea* Fl. Dan. Zeitschr. Bot. 3:381. 1911.

much the appearance of a multipolar spindle. These fibers bear no relation to the true spindle which now makes its appearance. No centrosomes were observed, and only four chromosomes of which two passed to either pole. The chromosomes changed greatly in shape as they moved along the spindle, indicating a very plastic nature. The second division follows at once, giving rise to the nuclei which pass into the spores. In some instances a third division takes place within the basidium, and as a result there is a degeneration of four of the nuclei.

FRIES[18] finds in *Hygrophorus conicus* that the cells of the trama contain one or more pair of nuclei, while the cells of the subhymenium have only a single nucleus, each having a conspicuous nucleole and two distinct masses of chromatin. Basidia, even the youngest, are uninucleated with the same double nature of the chromatic content. Growth of the basidium is accompanied by a corresponding growth in size of the nucleus, and the chromatin assumes the nature of a long delicate spireme thread. Following closely upon this there is a disappearance of the nuclear membrane and a sudden contraction of the spireme into a compact mass surrounded by a granular (plasma) cytoplasm. Spindle fibers now appear (no centrosome was found) and two chromosomes are seen to pass to each pole. The daughter nuclei, which at this stage lie near the apex of the basidium, are fully reconstructed and move toward the base of the basidium, where they remain while the sterigmata are developed. As soon as the sterigmata are fully formed, the nuclei in most cases become beaked and pass into the spore and divide; in other instances the division is partly completed in the basidium.

The first of these papers describes a process which is usually considered the typical method of nuclear behavior in the higher Basidiomycetes. We have here the fusion of nuclei, a synapsis, a spireme (double in its nature), a heterotypic followed by homotypic division.

In the second paper we have no fusion of nuclei, but stages are described and figures given which compare favorably with those of the preceding paper, although the author does not admit of chromosome reduction.

The third paper describes a form unique in that the cells of the trama contain more than one nucleus, while the basidium contains but one, and this according to the author is not a fusion nucleus. Therefore the division in the basidium is not a reduction division.—E. M. GILBERT.

Amanita.—Dr. RENÉ FERRY, former editor of the *Revue Mycologique*, has recently published a paper of a monographic nature dealing with the "deadly" Amanitas,[19] with special reference to their botanical characters,

[18] FRIES, ROB. E., Zur Kenntnis der Cytologie von *Hygrophorus conicus*. Svensk. Botanisk. Tidskrift 5: 242–251. 1911.

[19] FERRY, RENÉ, Étude sur les Amanites; les Amanites mortelles. *Amanita phalloides, Amanita verna*, et *Amanita virosa*. Rev. Mycologique. Suppl. 1. pp. 1–96. *pls. 1–8*. 1911. Saint-Dié (Vosges), France. 4.50 fr. On sale by the author.

chemistry, and toxicology. The first part is devoted to descriptions of the three species which the author believes are responsible for the deaths from mushroom poisoning: *Amanita phalloides*, *A. verna*, and *A. virosa*. *A. phalloides* is recognized as a very variable species. Good descriptions are given of these species and of the varieties of *A. phalloides*, and the determination of the species is further aided by colored illustrations, including the American varieties which are copied from PECK's Report. Not all students may agree with FERRY in his treatment of these species, but it is doubtful if anyone can at present, or even in the near future, limit and characterize the species of *Amanita* in a manner which will be acceptable to all. The author's object, however, is not so much to limit precisely the natural species as it is to present characters and illustrations by which the deadly species of this genus may be recognized by those who have little technical knowledge of the fungi.

The second part, covering more than 70 pages, is a thorough discussion of the recent work, in Europe and America, on the chemistry and toxicology of these three species, particularly of *A. phalloides*. There are two important toxic principles. Phalline (KOBERT) or "Amanita-hemolysine" (FORD) is a hemolytic agent which dissolves the red blood corpuscles. Its chemical nature is uncertain (FORD), but temperatures of 65–70° C. destroy it, so that thorough cooking renders this poison innocuous. The other toxic principle is "Amanita-toxine" (FORD), which is not destroyed by heat, and for which no antidote is known. Its chemical nature is unknown. Hemolysine is found in certain of the edible fungi, for example *Amanita rubescens*, and this emphasizes the necessity of thorough cooking of all mushrooms. There is a thorough discussion of the symptoms of poisoning by these toxins, treatment, precautionary measures, experiments on immunization, etc. The work is a valuable one for those interested in the determination of these poisonous species, and particularly for the physician, pharmacist, etc.—G. F. ATKINSON.

Jurassic cones.—NATHORST[20] has described two new species of the Jurassic cone-impression known as *Cycadocarpidium*, has established definitely its identity with the leaf-genus *Podozamites*, and has discussed the relationship of this interesting gymnosperm. The leaves (*Podozamites*) are linear or elliptical, and seem, in certain species at least, to be borne on definite short shoots. The sporophylls (*Cycadocarpidium*) are much like the vegetative leaves, and are arranged in loose cones. Each sporophyll bears at its base two ovules, with pointed, winglike appendages. *Cycadocarpidium*, at first believed to be the fructification of a cycad related to the Zamieae, is considered by the author as a possible connecting form between cycadophytes and conifers. A fuller knowledge of both the vegetative and reproductive structures of the plant, however, lends little support to the theory of its cycadean affinity, and it seems

[20] NATHORST, A. G., Über die Gattung *Cycadocarpidium* (Nathorst) nebst einigen Bemerkungen über *Podozamites*. Kungl. Svensk. Vetensk. Handl. **46**: no. 8. pp. 11.

best included among those strange mesozoic conifers of whose structure and relationships so much is yet to be learned.—E. W. SINNOTT.

The carpophore of Agaricaceae.—An investigation of the development of the carpophore of several species of the Agaricaceae by BEER[21] brings still further evidence supporting the now generally accepted view that the hymenium of the Agaricaceae arises endogenously, and not exogenously in the manner first described by HARTIG. As to the relative priority of the differentiation of the pileus and the hymenial primordium, BEER finds that in *Hypholoma fascicularis* and *Clitocybe laccata* the pileus is differentiated first, while in *Armillaria mellea* the hymenium is the first structure to become visible. In this respect *Armillaria mellea* agrees with *A. mucida* as described by FISCHER, and with *Agaricus campestris* as described by ATKINSON. These forms show that the generalization of FAYOD, that the pileus is first differentiated in all cases, does not hold for all forms.—H. HASSELBRING.

A paper atmometer.—In an effort to obtain an instrument for the measurement of evaporation with temperature relations comparable to those of the foliage leaf, LIVINGSTON[22] has devised a paper cup atmometer, which is a modification of the Piche instrument. The advantages claimed for the new device are that as it contains a much smaller volume of water than the porous cup atmometer, it responds more promptly to changes in the external temperature. The surface of the paper cup may also be colored and the atmometer used for the measurement of light effects. This form of atmometer is likely to prove most useful in exact laboratory and controlled experiments, but will not replace the more durable clay cup for ecological field studies.—GEO. D. FULLER.

Composition of soil water and plant distribution.—The percentage of calcium and magnesium salts in solution in the soil water is believed by LANGERON[23] to give adequate explanation for many local peculiarities of plant distribution. To facilitate such studies he describes methods of water analysis which may be used in the field and laboratory, giving, with a minimum expenditure of time and effort, results sufficiently accurate to be related to differences in the composition of various plant associations. He has obtained promising results by applying his methods to the study of the bryophyte flora of the Bouche d'Erquy.—GEO. D. FULLER.

---

[21] BEER, R., Notes on the development of the carpophore of some Agaricaceae. Ann. Botany **25**:683–689. *pl. 1.* 1911.

[22] LIVINGSTON, B. E., Paper atmometers for studies in evaporation. Plant World **14**:281–289. 1911.

[23] LANGERON, MAURICE, Valeur de l'hydrotimétrie en géographie botanique pour l'étude des accidents locaux. Bull. Soc. Bot. France **58**:236–245, 266–273, 327–336, 421–428. 1911.

GENERAL INDEX

Classified entries will be found under Contributors and Reviews. New names and names of new genera, species, and varieties are printed in **bold face** type; synonyms in *italic*.

D

E

F

G

H

I

J

K

L

V

W

X

Y

Z